Personality in wild juvenile lemon sharks: Consistency, behavioral syndrome and ontogeny

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CONTENTS

Summary

Consistent individual differences in behavior have been shown to be present in many different animal taxa and behaviors. These have been summarized within the term animal personality and have been shown to have consequences for the ecology and population management in some species. Little work has been done on large, wild animals such as sharks. In this thesis, I investigated different aspects of personality in juvenile lemon sharks (*Negaprion brevirostris*).

I repeatedly tested individuals in a novel open field test. This experiment showed that juvenile lemon sharks consistently differ in their behavior. In addition, repeated exposures to the novel open field, allowed me to demonstrate the presence of habituation. Habituation was used as an indication that this test can be used to investigate reaction to novelty. Finally, this experiment also revealed that individuals have variable rates of habituation.

Second, I tested consistent individual differences in some aspects of their social behavior over a few days up to a four-month period. While retesting individuals, group composition was changed to insure that repeatability was not due to the repetition of the same social environment between tests. Here again, I found that juvenile lemon sharks showed personality differences in their social behavior and this despite group composition changes and a four-month period between tests.

Third, I tested the presence of a behavioral syndrome between sociability and reaction to a novel open field while considering potential variation in this syndrome through ontogeny and locations of capture. In addition, I investigated the maintenance of individual differences in different age classes and locations of capture. I found a significant negative correlation between sociability and reaction to novelty in sharks from one of the two nurseries tested but only when they were older than a year. In addition, I found that young of year sharks did not demonstrate long term consistency in their behavior as opposed to older sharks.

Overall, this thesis contributes to the field of personality by having demonstrated the presence of consistent behaviors in a poorly studied taxon by investigating important questions from this field such as individual differences in plasticity, individuality in social groups, variation in behavioral syndromes and development of personality. The ecological consequences of such consistent behavioral differences between individuals are still poorly understood and remain an important aspect for future work.

Zusammenfassung

Dauerhafte Unterschiede individuellen Verhaltens wurden schon in vielen verschiedenen Tierklassen und Tierverhalten gezeigt. Dies wurde unter dem Begriff Tierpersönlichkeit zusammengefasst und es wurde gezeigt, dass dies Konsequenzen auf die Ökologie und das Bevölkerungsmanagement einiger Spezies hatte. Wenige Studien wurden darüber mit großen, wilden Tiere, wie die Haie, unternommen. In dieser Doktorarbeit behandle ich verschiedene Persönlichkeitsaspekte von jugendlichen Zitronenhaien (*Negaprion brevirostris*) .

Ich habe wiederholt Individuen in einem neuartigen Testfeld untersucht. Diese Experimente zeigten, dass jugendliche Zitronenhaie sich konstant verschieden verhalten. Außerdem konnte ich durch eine wiederkehrende Exposition in dem neuartigen Testfeld ein Gewöhnungsverhalten aufzeigen. Gewöhnung war ein Indikator, dass dieser Test es möglich macht, Reaktionen auf Veränderungen zu erforschen. Und endlich zeigte dieses Experiment dass Individuen verschiedene Gewöhnungsraten besitzen.

Zweitens testete ich konsistente individuelle Verschiedenheiten in einigen der sozialen Verhaltensweisen über Zeiträume von einigen Tagen bis Perioden von vier Monaten. Während des neuerlichen Tests von Individuen wurde die Zusammensetzung der Gruppen geändert, um sicher zu gehen, dass die Wiederholbarkeit nicht vom gleichen sozialen Umfeld zwischen den wiederholten Versuchen kam. Hier wiederum fand ich, dass jugendliche Zitronenhaie Persönlichkeitsdifferenzen in ihrem sozialen Umfeld besaßen und dies trotz der veränderten Gruppen und einer viermonatigen Periode zwischen den Tests.

Drittens testete ich die Präsenz eines Verhaltenssyndroms zwischen der Sozialisierung und der Reaktion auf ein neues Testfeld unter Berücksichtigung einer möglichen Variation dieses Syndroms durch Ontogenese und den Fangplatz. Dazu untersuchte ich noch die Dauerhaftigkeit von individuellen Unterschieden in verschiedenen Altersklassen und von verschiedenen Fangplätzen. Ich fand eine starke negative Korrelation zwischen der

Soziabilität und der Reaktion auf Ungewohntes bei den Haien, in einer von zwei getesteten Kinderstuben, aber nur wenn sie älter als ein Jahr waren. Dazu fand ich, dass Haie, die weniger als ein Jahr alt waren, keine langdauernde Verhaltenskonsistenz zum Gegensatz zu älteren Haien zeigten.

Zusammenfassend trägt diese Doktorarbeit zum Feld der Persönlichkeitsforschung bei, indem sie konstantes Verhalten in einer nicht sehr erforschten Tierklasse aufzeigt und dies durch die Untersuchung wichtiger Fragen in Bereichen wie die individuellen Unterschiede in der Plastizität, individuelles Verhalten in sozialen Gruppen, Variation bei Verhaltenssyndromen und der Entwicklung von Persönlichkeit. Die ökologischen Konsequenzen von solch konsistenten Verhaltungsunterschieden zwischen Individuen sind immer noch schlecht verstanden und bleiben ein wichtiger Aspekt für zukünftige Forschung.

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1. General Introduction

1.1 AIM AND OUTLINE

While interacting with other persons, one can often identify predictable behavioral differences between individuals. This predictability allows us to define them with numerous adjectives (e.g. bold, curious, introvert, social) which fall into the more general term of personality. Similarly, such predictable, consistent individual differences have been described in a wide range of animal species (Bell et al., 2009; Gosling, 2001; Réale et al., 2007; Sih et al., 2004a; Sih et al., 2004b). However, in some taxa, individuality remains a poorly investigated facet of their behavior. Such is the case for sharks, the model taxon of this thesis. Therefore, the main aim of this thesis is to investigate the presence of personality in a wild population of juvenile lemon sharks.

It is undeniable that this thesis focused on sharks. However, it is worth noting that the different experiments conducted here relate to contemporary questions in animal personality in general. C**hapters 2, 3 and 4** describe the experimental work that was done in Bimini. The thesis begins with a general introduction in which I introduce personality and present the nomenclature and definitions used in this study. I, then, describe the current state of knowledge in the area of shark personality. It is then followed by a description of the juvenile lemon shark's ecology highlighting this species as an interesting model to study personality in a wild population of sharks. Finally, the thesis ends with a general discussion. First, I discuss the difficulty of uniting results from the animal personality field by comparing my methods/model species with other studies. Then I focus on the importance of personality in the ecology and conservation of animals. These two parts of discussions demonstrate the importance of continuing research in sharks and therefore the second half of the discussion focuses on the need and feasibility to study personality in wild shark populations. This is done

by a succinct review of shark field studies describing individual differences in their natural behaviors. It specially focuses on behaviors that are likely to be influenced by the traits we have tested in my different experiments. The potential ecological consequences and theoretical implication of these individual differences are discussed. Finally, I propose tools and methods that could further help the investigation of personality in sharks in future.

1.2. ANIMAL PERSONALITY

Personality in animals describes consistent behavioral differences between individuals of the same population across time and contexts (Stamps & Groothuis, 2010) and has become of major area of interest for behavioral ecologists. This popularity is, to some extent, due to the change in perception of variations around population averages of behavior. Indeed, when individual differences are no more random noises but are consistent, these differences can have significant consequences in the evolution, ecology and population management of animals (Biro & Sampson, 2015; Dochtermann & Dingemanse, 2013, Mittelbach et al., 2014; Sih et al., 2012; Wolf & Weissing, 2012). However, this fast-growing interest has led to a high diversity in terminology and definitions (e.g. Carter et al., 2013; Gosling, 2001; Réale et al., 2007) which makes clarification of terms used in this thesis necessary.

Animal personality can be approached from different perspectives and levels. For instance, individuals can consistently differ in certain behaviors, referred to hereafter as behavioral or personality axes. Five axes are commonly used which provide a framework to explore animal personality (Réale et al., 2007). These have been termed (1) shyness-boldness being an individual's reaction to a risky situation (e.g. predator, human), (2) exploration-avoidance being an individual reaction to novelty, (3) activity being the general level of activity, (4) aggressiveness being individual agonistic behavior to conspecifics and (5) sociability being the individual reaction to the presence or absence of conspecific. As described by Réale et al. (2007), this terminology is a simplification and should be improved

as research advances. Still these exclusive definitions avoid confusion between terms and therefore provide a useful framework to investigate personality. For instance, in this work, being able to differentiate between activity and reaction to novelty is important for the correct interpretation of personality tests used (see **chapter 2**). As more methods are being developed and more species are being screened for personality, this classification can be improved either by adding categories or merging terms. For instance, sociability might be too general and behaviors such as leadership or tendency to socialize might not be measuring the same sociability behavioral axis (see **chapter 3**). One other useful point with using such classification of behavioral axes is the possibility to investigate different sets of correlations between them (usually termed behavioral syndromes). For instance, a positive correlation between boldness and aggressiveness has been described before (Bell & Sih., 2007; Huntingford, 1976). Interestingly, recent studies suggest strong variations in the direction, strength and even presence of these correlations across and within species (Bell & Sih., 2007; Dingemanse et al., 2007; Garamszegi et al., 2013; see **chapter 4**). Therefore, using discrete axes allows investigators to test different behavioral relationships and build workable hypotheses based on the ecology of the target species. In this thesis, I will use the term behavioral syndrome to define correlations or covariances between any of the behavioral axes mentioned before. I use the term animal personality as a general notion that encompasses both behavioral axes and syndromes.

1.3 PERSONALITY IN SHARKS

Sharks are part of a highly diverse group of marine vertebrates, known as the cartilaginous fishes (Chondrichthyes). Chondrichthyans evolved independently of bony fishes (Osteichthyes) at least 400 million years ago (Pough et al., 1999) and, therefore, should not be considered “typical” fish (Sims, 2003). The vertebrate class Chondricthyes includes Holocephali (Chimaeras) and elasmobranchs (sharks, skates, and rays). Sharks range from

planktivores to apex predators, exhibit diverse modes of reproduction, display ontogenetic shifts in their diet and habitat selection, and show considerable variation in brain size and complexity (Grubbs, 2010; Lowry & Motta, 2008; Yopak, 2012; Yopak et al., 2007). A large proportion of shark species present slow growth and reproduction rates, and long-life spans. Their diversity, important functional roles in the top-down control of marine ecosystem structure and function (Ferretti et al., 2010; Heithaus & Dill, 2002), and life history strategy make them an interesting taxon to study relative to most aquatic animals commonly investigated in animal personality, e.g., guppies (*Poecilia reticulata*; Burns, 2008; Irving & Brown, 2013), mosquitofish (*Gambusia spp.*; Burns et al., 2012; Cote et al., 2010), and sticklebacks (*Gasterosteus aculeatus*; Harcourt et al. 2009a; Ward et al. 2004). In addition, due to these life history traits and overexploitation in global fisheries, many shark populations are in decline (Dulvy et al., 2014; Worm et al., 2013) which might, in turn, impact entire ecosystems through trophic cascades and interactions (e.g. Heithaus et al., 2008; Stevens et al., 2000). These environmental concerns combined with the recent realization that personality should be included within environmental and fishery management programs (Conrad et al., 2011; Mittelbach et al., 2014) argue for a better understanding of shark behavior at the individual level.

To date, only a handful of studies have investigated elasmobranch personality and they all occurred in the time frame of this thesis. They have focused on testing for the presence of personality traits in a few shark species. In addition to the lemon shark from Bimini, Bahamas, personality has also been studied in the Port Jackson shark (*Heterodontus portusjacksoni*; Byrnes & Brown, 2016; Byrnes et al., 2016a), the small-spotted catshark (*Scyliorhinus canicula*; Jacoby et al., 2014) and another population of juvenile lemon shark (Wilson et al., 2015).

As is the case for most animals, sharks reared in captivity are more readily accessible for behavioral assays and personality investigations than their wild counterparts. Taking advantage of the ability of juvenile small spotted cat sharks to thrive in captivity, Jacoby et al. (2014) investigated consistent individual differences in their social network positions. Catsharks are a small-bodied benthic species, regularly observed resting on the seabed in social groups (Jacoby et al., 2014; Sims et al., 2001). Such grouping can be defined as socially connected when one shark rests within one body length of another. This obvious and easily observable social behavior allows for the construction of social networks (Croft et al, 2011; Krause et al., 2009). Social network analyses provide measures to characterize the social dynamic of groups. Within these measures, some are focused on individuals, and so provide a method for quantifying individual sociability or social personality. Jacoby et al. (2014) repeatedly tested groups of the same individuals across different habitat types e.g. simple to complex. They found that individual social association strength (sum of an individual's association index with all other individuals) was consistent across habitats. However, when preference for group size was controlled for (average group size each individual was observed in), the consistency in social behavior was less pronounced and no longer significant, suggesting that group size preferences drive social consistency, but only within small groups. In their discussion, the authors suggested rearranging individuals between test groups to determine if this consistency was due to individual personality or the group dynamic (average group size available). This would certainly be an important next step to investigate for this species and would help to elucidate the role of personality traits in grouping behavior of a marine predator (see also **chapter 3**).

To test for consistency in social network position, Wilson et al. (2015) observed ten wild-caught juvenile lemon sharks from Eleuthera, Bahamas, in a mangrove enclave that was artificially closed. Individuals equipped with tri-axial accelerometer loggers were observed

three times a day over eight days for their sociability (i.e., being within 1 body length of a conspecific) and leadership (i.e., being at the front of a pair or group), as well as locomotor profile (e.g., time swimming fast, swimming duration, frequency of burst swimming events, number of transitions between activity states, activity period). In contrast to catsharks assessed previously, juvenile lemon sharks in this experiment did not show consistent differences in their network positions. The dynamic of social interactions was related to individuals' locomotor profiles. Furthermore, the authors found that more social individuals were more active than less social individuals. This relationship between sociability and activity level might indicate the presence of a behavioral syndrome similar to that observed in bony fishes (e.g., Cote et al., 2010; Irving & Brown, 2013). However, this remains to be demonstrated due to the lack of consistency in social behavior and the fact that the behaviors were not tested independently, thus creating a contextual overlap (Garamszegi et al., 2013).

To investigate the presence of consistent individual differences in an emergence test and stress responses to handling, Byrnes and Brown (2016) collected wild Port Jackson sharks and housed them temporarily in a laboratory. Sharks were scored based on time taken to move out of cover from a "refuge box" (emergence test) and the increase or decrease in activity relative to their baseline activity (reaction to stress test). The sharks showed consistent individual differences in both tests across repeated testing. Furthermore, the sharks that emerged faster from cover, i.e., bolder individuals, were more active after handling compared to those that were less bold. The authors interpreted this as evidence for the existence of a proactive-reactive coping style in sharks, with reactive individuals being more passive toward their environment than were proactive individuals. In addition, individuals that were more active after a stressful event exhibited greater lateralization strength, i.e., the propensity to choose one turning direction over another compared to individuals that were less active (Byrnes et al., 2016a). Due to the lack of comparative data in elasmobranchs, these

relationships are difficult to interpret. Taken together, however, these early findings offer guidelines that could be applied to studies of different shark species, enabling other researchers to gather much-needed data to draw conclusions about the evolution of personality in sharks and other elasmobranchs.

Evidence for personality was recently demonstrated in a study that involved capturing and testing Port Jackson sharks in the field (Byrnes et al., 2016b). The researchers used a docility test that measured the sharks' response to human handling (e.g., Martin & Réale, 2008), and a lateralization test that recorded if and which side a shark rolled onto once it landed on a boat. Individuals consistently differed in docility, varying from sharks that struggled to those that did not move during handling, despite controlling for potential confounding effect of size, sex and population. Consistency of lateralization was not investigated due to the lack of repeated trials, but individual differences were detected. The authors found no covariance between these two tests. This study thus described a new method of assessing personality that is applicable to numerous species, including bottom dwelling sharks, such as nurse sharks (*Ginglymostoma cirratum*) or catsharks. Using this study as inspiration could lead to a large comparative data set based on observations in the wild and provide an interesting avenue to test for personality in relation to natural shark behavior. However, the approach used here would have to be modified for larger and/or more mobile animals.

1.4 JUVENILE LEMON SHARK

These former studies and especially their low number illustrate the novelty of the study of personality in sharks. Indeed, this field is still at the stage of demonstrating the mere presence of personality in the different species tested along with validating methods. The development of models and methods is unquestionably a capital step to take and accordingly is one of the main objectives of this thesis. Due to its behavior and ecology, developing juvenile lemon

shark of Bimini as a model species could be beneficial to the study of shark and animal personality. In Bimini, during their first three years of life, juvenile lemon sharks use nursery areas (mangrove fringed lagoons) as protection from predators (Chapman et al., 2009; Guttridge et al., 2012). They have small home ranges and display high site fidelity (Morrissey & Gruber, 1993a, 1993b; Sundström et al., 2001). Interestingly, acoustic telemetry studies revealed excursions out of the typical home range into deeper water, and away from the safety of the mangroves (Morrissey & Gruber, 1993b) and visual observations have shown differences in refuge use (Guttridge et al., 2012). In addition, the social behavior of these sharks has been extensively studied (Guttridge et al., 2009; Guttridge et al., 2011; Guttridge et al., 2013) and individual differences have been observed (TL Guttridge, personal communication). Therefore, these studies provide a solid base to investigate individual differences in movements, social behavior and by extension the presence of a syndrome between these two axes.

Furthermore, annual sampling of the majority of a population allows for the long-term study of their ecology (e.g., life history: Dibattista et al., 2007; philopatry: Feldheim et al., 2014; survival: Gruber et al., 2001) along with changes through ontogeny. Therefore, this system represents an unusual opportunity to investigate ontogenetic variations and long-term stability in personality of wild and large marine animals.

Interestingly, it has been demonstrated that large and fast-growing one-year old lemon sharks have a higher mortality rate (Dibattista et al., 2007), which supports the idea that higher risks bring greater benefits (i.e., increased growth for higher mortality). In addition, stable isotope analyses in juvenile lemon sharks from Bimini revealed pronounced individual differences in their feeding habits (Hussey et al., 2017). Some sharks preferentially feed close to shore (mangroves; refuge habitat) whereas others have a wider range (including seagrass flats; risky habitats). Although none of these investigations explicitly tested personality, their

observations indicate possible individual differences in the inclination of sharks to take risks for more benefits. This balance between risk and benefits is a common hypothesis for the explanation of individual differences (Stamps, 2007; Wolf et al., 2007) and could play a major role in explaining the presence of personality in the juvenile lemon shark of Bimini. This is still hypothetical, as these studies have been performed independently.

Overall if methods can be developed and personality is demonstrated in juvenile lemon sharks, I believe that the juvenile lemon shark has the potential to become an interesting model for the study of sharks and potentially other large marine animals' personality.

1.5 EXPERIMENTS

For this I used captive experiments that would, to some extent resemble interesting natural behavior already described in this species. Because movement and exploration (excursion out of home ranges) seem to be present in juvenile lemon sharks, I thought of novel open field test as a promising method for this species (**Chapter 2**). Similarly, the investigation of individual differences in sociability seemed promising (**chapter 3**). Finally, because these two tests were developed for this thesis, I could also investigate the presence of a behavioral syndrome between these two traits (**chapter 4**).

In addition, to further validate the method and interpretation of these tests, each chapter extended beyond the demonstration of personality. While investigating reaction of sharks to a novel open field (**chapter 2**), I was also interested in understanding what we were measuring in this test. Indeed, novel open field test is a commonly used test for many taxa (e.g. Boon et al, 2007; Budaev, 1997; Burns, 2008; Dingemanse et al., 2012; Rodríguez-Prieto et al., 2010; Verbeek et al., 1994) but can be interpreted differently (e.g. Toms et al., 2010; Réale et al., 2007) and only a few studies are concerned with interpreting personality tests in animals. I tested if movements recorded were a proxy of activity or reaction to novelty

(*sensus* Réale et al., 2007)? To answer this question each individual was exposed six times to the novel pen to test for the presence of habituation to novelty. This also allowed me to investigate if habituation rates differed between individuals and these differences were related to individual personality.

To measure social personality in juvenile lemon sharks, I decided to observe individuals freely interacting in social groups (**chapter 3**; e.g. Krause et al., 2017), instead of using binary choice (e.g. Cote et al., 2010; Guttridge et al., 2009; Harcourt et al., 2009a). While doing so I was also interested in the maintenance of individual differences in their sociability despite group composition changes. This aspect has been poorly investigated despite being a potential critical point especially in fission-fusion societies.

In order to investigate the presence of a behavioral syndrome in a wild population, one has to consider the environment components and age classes to avoid type-II error and reject an existing behavioral syndrome. Indeed, recent studies have demonstrated strong variation in behavioral syndromes even within the same species. Therefore, while I was testing the presence of a behavioral syndrome I was also interested in variation in syndrome within the studied population. In accordance with the lemon shark ecology, I differentiated individuals based on their location of capture and their age classes. Testing different age classes also allowed me to look at the maintenance of individual differences over long time periods within them. Therefore, along with behavioral syndrome, **chapter 4** also includes investigations on personality and BS development throughout ontogeny.

2. Rate of movement of juvenile lemon sharks in a novel open field, are we measuring activity or reaction to novelty?

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Personality differences are widespread throughout the animal kingdom and can have important ecological and evolutionary consequences. Despite a rapidly increasing body of literature, large (marine) vertebrates remain underrepresented in personality research. Given their unique life history traits (e.g. slow growth rate, slow reproduction rate, long life span) and their pivotal role in ecosystem processes, this is an important gap in our current knowledge. Here we investigated consistency and plasticity in movement behavior of wild juvenile lemon sharks, *Negaprion brevirostris*, by repeatedly subjecting sharks to open field tests. First, we investigated the presence of inter-individual differences in movement behavior in a novel open field. Second, we investigated the effect of trial repetition on movement behavior to understand whether movement in a novel open field reflects a reaction to novelty, or general activity. Third, we estimated individual differences in habituation/sensitization rates over trial repetition and studied how the habituation rate was predicted by the initial movement rate. We found consistent individual differences in movement behavior during the open field tests. Sharks showed habituation in movement behavior (i.e. decrease) over repeated trials indicating that the movement behavior during the first trials is a reaction to novelty, and not general activity. Individuals, however, differed in their rate of habituation (i.e. plasticity) and this rate was negatively related to an individual's movement behavior in the first open field trial. In addition to showing individual differences in consistency and plasticity in juvenile lemon sharks, our study emphasizes the importance of examining the validity of personality tests when adapting them to new species.

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INTRODUCTION

The discovery that individuals can show consistent behavioral differences through time (i.e. animal personality; Biro & Stamps, 2008) has shifted the traditional view of individual variation from random noises to a biologically important phenomenon. Indeed, such differences in individual behavior can have important ecological and evolutionary consequences (Sih et al., 2004a; Wolf & Weissing, 2012) and enhance management programs (Conrad et al., 2011; Mittelbach et al., 2014). As a result, research on animal personality is currently booming and knowledge is rapidly accumulating on a diversity of species (Gosling, 2001; Réale et al., 2007; Sih et al., 2004b). However, despite this rapid expansion much of our understanding comes from studies on captive animals that are easy to house and with a short life span (Archard & Braithwaite, 2010). This bias has led to an underrepresentation of large animals, especially large marine vertebrates which are usually characterized by slow growth rate and reproduction rate, long life span and a relatively high trophic position (Jenning et al., 2001; Lewison et al., 2004; Romanuk et al. 2011; Stevens et al., 2000). These characteristics make them both important to ecosystems processes and highly vulnerable to anthropogenic impact (Estes et al., 2011; Stevens et al., 2000). Furthermore, obtaining data on a wide variety of organisms with different life history and ecological conditions is warranted to understand the evolution of animal personality (Réale et al., 2007; Réale et al., 2010). Therefore, expanding personality research to animals with longer life spans is vital.

Advancing knowledge of large aquatic organisms is challenging because of logistical constraints (e.g. sample size, capture constraints, housing difficulties). However, novel technologies such as biotelemetry (radio and acoustic telemetry) and biologging (archival logger) devices now offer sophisticated means of evaluating the behavior, spatial ecology, energetics and physiology of these animals in their natural environment (Cooke et al., 2004; Hussey et al., 2015; Krause et al., 2013). In recent years, applying these techniques has led to

the discovery of individual variation in movement patterns, habitat use and feeding habits for various large marine animals, such as mammals, sharks, birds and reptiles (Hatase et al., 2007; Heithaus et al., 2002; Kuhn et al., 2009; Matich & Heithaus, 2015; Patrick et al., 2014; Rosenblatt & Heithaus, 2011; Tinker et al., 2007; Vaudo et al., 2014). The observed individual differences, however, cannot easily be directly linked to personality due to the challenge of disentangling personality from various other factors (e.g. environmental or population differences). It is, therefore, pertinent to develop appropriate captive personality tests that complement these field data. Such experiments have been adapted successfully for sharks, identifying social personalities in catsharks and showing the importance for their social structure of individual differences in the locomotion behavior of juvenile lemon sharks (Jacoby et al., 2014; Wilson et al., 2015). However, the development of standardized tests to detect consistent individual differences in sharks' movements is still lacking. The 'open field test' has frequently been used to quantify consistent individual differences in movement and is, therefore, a promising candidate to investigate personality in sharks.

Developing and interpreting personality tests can be challenging (Carter et al., 2013) and open field tests are no exception. In their seminal study, Réale et al. (2007) proposed five distinct personality axes: aggressiveness, sociability, shyness–boldness, exploration–avoidance (also called neophilia) and activity. Within these axes, the behaviors during open field tests have mostly been interpreted as exploration (Conrad et al., 2011; Garamszegi et al., 2013) but also as boldness (Toms et al., 2010) and, when distance moved is recorded, as activity (Carter et al., 2013). Various methods can help to interpret behavior during personality tests. Carter et al. (2013) discussed the use of convergent (i.e. different tests measure the same personality trait) and discriminant validity tests (i.e. different tests measure different personality traits). For example, in guppies, movement activity in an open field test was not correlated with activity in a nonstressful environment (Burns, 2008), suggesting that

the open field test measures reaction to novelty and not general activity (i.e. discriminant validity). However, in this study (and for large vertebrates in general) performing multiple tests was logistically difficult.

Another method to verify a reaction to novelty is to repeatedly expose individuals to the same open field (Warren & Callaghan, 1976). If the observed behavior is a reaction to novelty, it is expected to covary with the number of exposures (i.e. habituation and/or sensitization; Groves & Thompson, 1970). Thus, when facing logistical constraints, testing habituation and/or sensitization can be a viable alternative. In addition, several studies have demonstrated high individual variation in the strength and direction of the response change, with such variations being related to an individuals' personality (Mathot et al., 2012). Personality-related differences in plasticity (also known as behavioral reaction norms) have gained attention because of their evolutionary and ecological significance (Dingemanse et al., 2010; Dingemanse & Wolf, 2013; Martin & Réale, 2008; Mathot et al., 2012). Thus, when repeatedly exposing individuals to the open field, it is possible to also investigate the presence of individual differences in plasticity and its effect on repeatability.

In this study, we used the lemon shark, a common large coastal species in the western Atlantic whose biology, behavior and ecology have been extensively studied (Guttridge et al., 2009, Guttridge et al., 2012, Sundström et al., 2001). At our study site in Bimini, Bahamas, juveniles (<4 years) use the mangrove-fringed shoreline which offers a shallow (< 0.5 m depth) and protected habitat (Newman et al., 2007). Adjacent to the shorelines are deeper seagrass flats which older conspecifics (> 120 cm total length) occupy during favorable tides to predate upon the juveniles (Guttridge et al., 2012; Morrissey & Gruber, 1993a). Despite having a home range close to the shoreline, some juvenile lemon sharks venture into these riskier habitats (Morrissey & Gruber, 1993b). Dibattista et al. (2007) demonstrated that sharks that were large at birth and fast growing had higher mortality rates than smaller, slower

growing individuals. These findings, together with their ease of capture, abundance and robustness in captivity, make the lemon shark an excellent model species for cartilaginous fishes and large marine vertebrates to experimentally investigate individual differences in a novel open field.

Juvenile lemon sharks were observed on six occasions in an open field, with the following aims: (1) to test the repeatability of their rate of movement (ROM) to investigate the presence of interindividual differences in movement behavior; (2) to test the variable ROM for habituation and/or sensitization with repeated exposure to the open field to understand whether the behavior is a proxy for activity or for reaction to novelty; and (3) to investigate the presence of individual differences in the strength and/or direction of such a habituation/sensitization effect and how differences in these effects, in turn, relate to personality.

METHODS

Study site and experimental set-up

This study was conducted in Bimini (20°–28°N, 72°–80°W), Bahamas, a chain of islands situated approximately 85 km east of the coast of Florida, U.S.A. In total, 28 juvenile lemon sharks (14 females and 14 males) were captured using gillnets (see Manire & Gruber, 1991 for details). Upon capture, each individual was measured for body size (mean precaudal length (PCL) ± SD = 53.23 ± 4.79 cm), sexed and equipped with a unique colour-coded tag (T-bar type, Floy Tag Inc, Seattle, WA, U.S.A.) for visual identification.

Sharks were housed in a large circular holding pen (10 m diameter) constructed just offshore in shallow (<1.5 m) sand bottom flats (see Guttridge et al., 2009 for details). Sharks were given a minimum of 2 days to acclimatize to captive conditions. During non-experimental periods, sharks were fed to satiation every 3 days on a diet of fresh and frozen

local fish (*Sphyraena barracuda*). During experimental periods, sharks were always fed the day before an observation day (see below).

Secured to the holding pen was a start box (semicircle; 1.5 m radius) that provided access to a rectangular (6 x 12 m) open field split into 18 sectors (2 x 2 m) by ground markers (Fig. 1). Sliding doors (manually operated) were used to control the movement of sharks between the three compartments, with an external exit channel attached to the test pen to facilitate the return of sharks after trial completion. Individuals had never been introduced to this pen before the trials. Behavioral observations were conducted from a 2 m high observation tower.

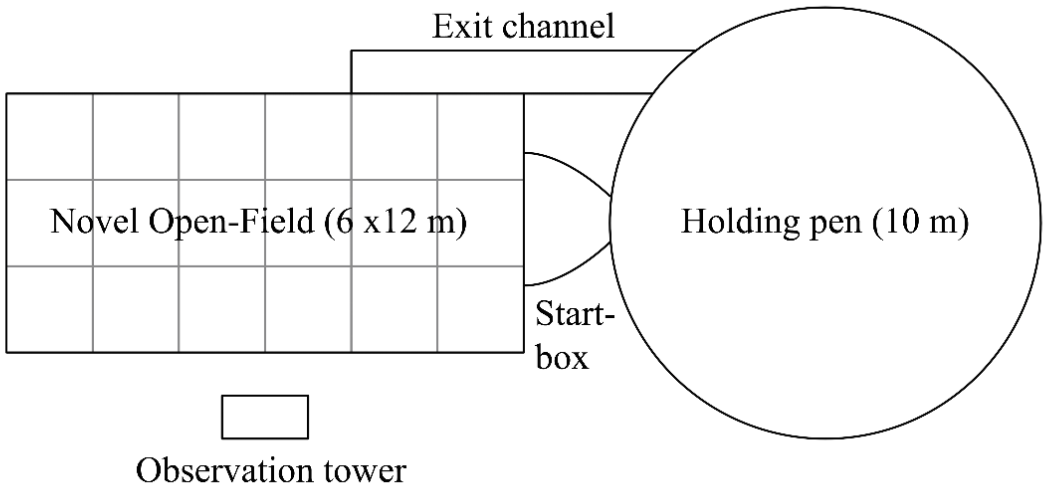

Figure 1: Schematic overview of the experimental set-up used for testing the movement behavior of juvenile lemon sharks in a novel open field.

Experimental procedure

Prior to the test, a predetermined shark was ushered into the start box. After 5 min, the sliding door was opened, allowing the shark to enter the test pen. The door to the start box was then gently closed. The shark was observed in the test pen for 10 min, during which the total number of sectors visited was recorded as a measure of the shark's ROM, as well as the total

number of new sectors visited. Sharks were recorded as having entered a sector once their head and first dorsal fin crossed the demarcation line. Upon trial completion, the shark was ushered back to the holding pen via the exit channel. Each shark completed six trials, one every 2 days across a 12-day period. If observations from the tower were not possible due to inclement weather (e.g. rainstorms), sharks were still subject to the same procedures and these trials (N = 7, < 5%) were treated as missing values. For two trials environmental values were not taken (see below). These trials were also excluded resulting in 159 trials for 28 individuals.

All trials were conducted at least 2 h after sunrise and before sunset to avoid luminosity biases. The exact timing of each trial was scheduled using tide predictor software (WXtide32: http://www.wxtide32.com), to minimize any potential effects of differences in water depth between trials (mean ± SD = 55 ± 5.5 cm) and to retain the same current direction (rising tide). Therefore, the number of animals tested per day was restricted to a maximum of three. By alternating two groups of the maximum three individuals each day, six individuals could be observed across a 12-day period. However, depending on the number of animals captured during gillnetting some of these periods contained fewer than six individuals. In total there were six of these 12-day periods. For each trial, percentage cloud cover, underwater visibility (using a Secchi disc) and wind speed were recorded and controlled for in the following analyses.

Data analysis

Statistical analyses were only applied to ROM due to the very low variation in the total number of new sectors visited (the first quartile and the median were the maximum: 18 sectors). ROM was square root transformed and checked for normality using a Shapiro test. All statistical procedures were performed in R v3.2.3 (R Core Team, 2015) using the lme4 package for mixed models analysis (Bates et al., 2015). Significance levels were derived

using the package lmerTest (Kuznetsova et al., 2015) based on Satterthwaite's approximations.

Repeatability

To test for repeatability in ROM, a linear mixed model was used with ROM as response variable, shark ID as random factor and trial number (continuous: 1–6), time period (number of days since the start of the experiment; continuous: 1–75), body size, sex, wind speed, cloud cover, time in captivity (continuous: 2–33 days) and visibility as fixed effects. The significance of the random term was assessed using the function exactRLRT from the package RLRsim (Scheipl et al., 2008) with 10 000 simulations. Finally, repeatability was calculated by dividing the individual variance by the total variance (individual plus residual variance). To test for a potential effect of habituation on repeatability, we performed similar analyses using subsets of the data: (1) trials 1 and 2, (2) trials 1 and 6 and (3) trials 5 and 6.

Individual variation in habituation/sensitization

To test for the significance of personality-related differences in habituation/sensitization, a random slope mixed model with the interaction between trial number and shark ID was compared to a similar model but with only shark ID as random term. A likelihood ratio was calculated between these two models and significance was assessed against a chi-square distribution of two degree of freedom. Finally, repeatability was calculated by dividing the variance explained by shark ID by the total variance of the random slope mixed model (shark ID, Residuals and Slope variance), using the same response variables as described above.

To improve the interpretation of our random slope mixed model analysis, we carried out a power analysis. We performed a similar analysis as described above using only trial number as a fixed effect. The parameters obtained were used in the PAMM package (Martin

et al., 2011). We allowed the number of simulated individuals to vary between 20 and 100 (increments of 10), keeping the number of replicates fixed at six.

Owing to the lack of power (see Results), we used a second method to investigate the relationship between personality and differences in plasticity. The effect of trial number on ROM was linearly regressed for each individual and the slope was extracted as an estimate of an individual's habituation/sensitization rate. To investigate the relationship between ROM during trial 1 and this habituation/sensitization rate, a linear regression was used with habituation/sensitization rate as dependent variable and ROM scores from trial 1 as an independent variable. Body size, time period, time in captivity before trial 1 (continuous 2–22 days) and sex were included as fixed effects. Lastly, we investigated the relationship between ROM in trial 1 and habituation/sensitization rate using a Spearman rank correlation test.

RESULTS

Repeatability

Juvenile lemon sharks showed consistent individual differences in their ROM when including all trials (repeatability = 0.28; restricted likelihood ratio test, restricted likelihood ratio = 16.3, $N = 28$, $P < 0.001$). ROM decreased with the number of trials showing an overall effect of habituation. Further, body size, cloud cover and time period significantly affected ROM; however, there were no significant effects of sex, wind speed, visibility or time in captivity (Table 1).

Table 1: Results of a linear mixed model testing the effects of several fixed effects on the rate of movement (ROM) in an open field over six repeated trials with individual as random factor

Variable	Estimates ± SE	*df*	*t*	*P*
Intercept	11.00 ± 1.02	24.27	10.82	**<0.001**
Trial number	-0.074 ± 0.027	128.04	-2.75	**<0.01**
Body size	0.053 ± 0.018	23.28	2.95	**<0.01**
Cloud cover	0.003 ± 0.0015	139.02	2.01	**0.046**
Time period	0.0083 ± 0.0035	26.01	2.33	**0.028**
Time in captivity	0.015 ± 0.014	23.08	1.07	0.30
Visibility	-0.078 ± 0.045	141.32	-1.75	0.083
Sex (male)	-0.088 ± 0.183	22.93	-0.48	0.63
Wind speed	-0.0043 ±0.0073	135.58	-0.588	0.56

Bold values indicate *P* values below 0.05.

Interestingly, sharks showed consistent individual differences when trials 1 and 2 were compared, no consistent differences comparing trials 1 and 6 and a trend comparing trials 5 and 6 (trials 1 and 2: repeatability = 0.50; restricted likelihood ratio test, restricted likelihood ratio = 5.02, $N = 26$, $P = 0.01$; Fig. 2a; trials 1 and 6: repeatability = 0.03; restricted likelihood ratio test, restricted likelihood ratio = 0.01, $N = 26$, $P = 0.45$; Fig. 2b; trials 5 and 6: repeatability = 0.39; restricted likelihood ratio test, restricted likelihood ratio = 2.01, $N = 26$, $P = 0.08$; Fig. 2c).

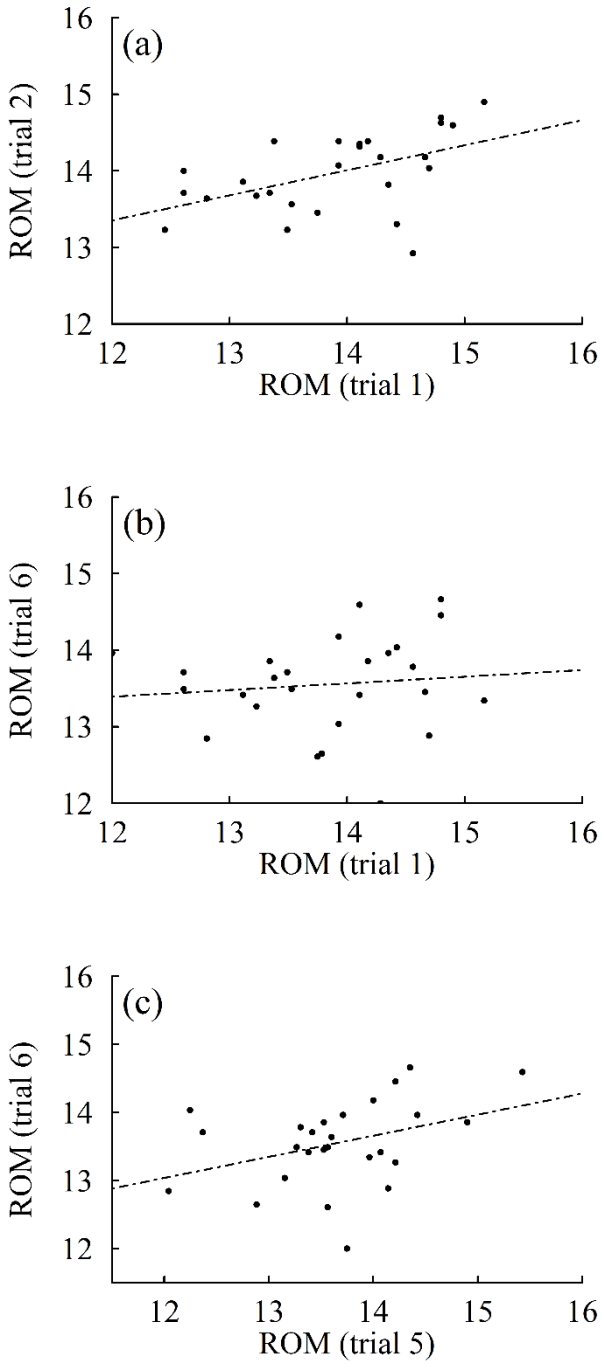

Figure 2: Comparison of lemon sharks' rate of movement (ROM) in (a) trials 1 and 2, (b) trials 1 and 6 and (c) trials 5 and 6. Square root transformed ROM values were used to draw the linear regression lines.

Individual variation in habituation/sensitization

The random slope mixed model analyses suggest that individuals did not differ significantly in their rate of habituation/sensitization (likelihood ratio test, likelihood ratio = 1.68, $N = 28$, $P = 0.42$) despite a high correlation estimate between individuals' intercepts and slopes (correlation: -0.78). When individual variation in plasticity was accounted for, the repeatability score obtained was 0.51. We obtained similar results when only including trial number as response variable (likelihood ratio test, likelihood ratio = 5.51, $N = 28$, $P = 0.063$; correlation: -0.76). This lack of significance should, however, be taken with caution as additional simulations show that the power, obtained with our sample size, is rather low (Fig. 3).

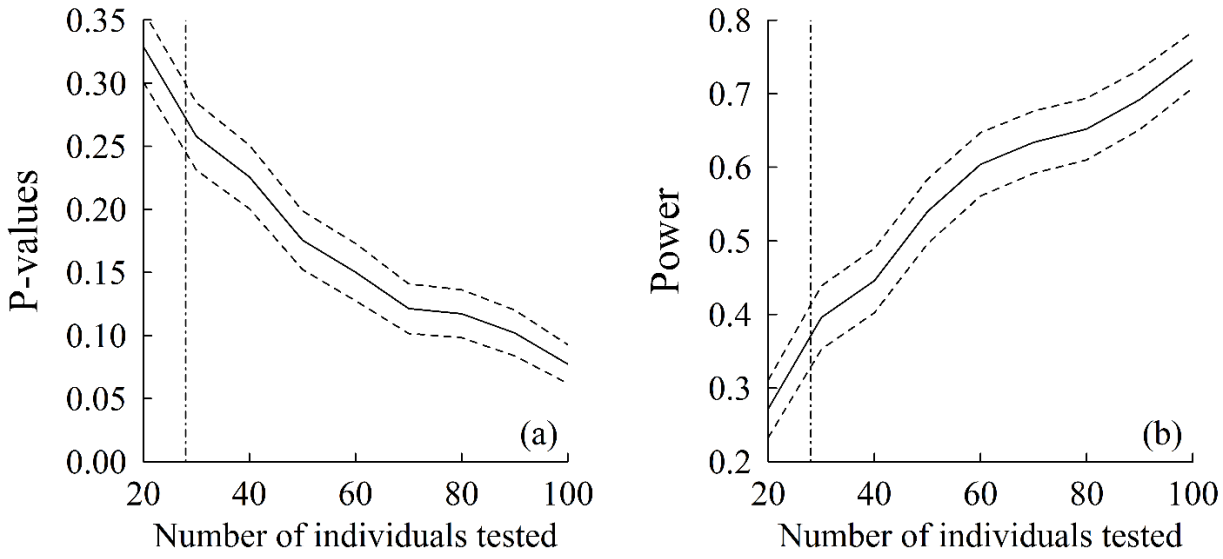

Figure 3: (a) Simulated *P* values and (b) power analysis to detect the significance of the random slope as a function of the number of individuals tested. This simulation was based on random slope mixed model results obtained in this study and with the number of replicates per individual fixed at six. Vertical lines represent the actual sample size ($N = 28$).

Using the simpler linear regression analysis, we found that the habituation/sensitization rate covaried negatively with the increase in ROM during trial 1 (estimate ± SE = -0.16 + 0.035;

Student t test: t_{22} = -4.506, P < 0.001; Fig. 4). Interestingly, sharks ranged from either a decrease, increase or no change in ROM over trial repetition. Furthermore, time period had a significant positive effect on the habituation/sensitization rate (estimate ± SE = 0.003 ± 0.001; Student t test: t_{22} = 2.702, P < 0.05). There was no significant effect of time in captivity before trial 1, sex or body size (all P > 0.05). In addition, when using the Spearman rank test, we found a negative correlation between ROM during trial 1 and the habituation/sensitization rate (Spearman rank correlation: r_S = -0.55, N = 28, P < 0.01).

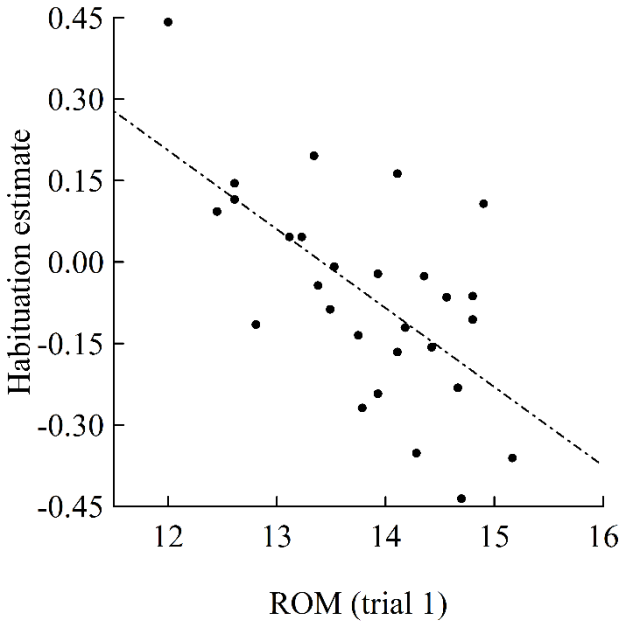

Figure 4: The rate of movement (ROM) during trial 1 in relation to the subsequent rate of habituation/sensitization. Negative values indicate habituation (i.e. decrease in movement activity); positive values indicate sensitization. Square root transformed ROM values were used for a linear regression.

DISCUSSION

Our results show that juvenile lemon sharks have consistent individual differences in their rate of movement (ROM) when tested repeatedly in an open field. In addition, we found that ROM in a novel open field can be used as a proxy for reaction to novelty since a decrease (i.e.

habituation) was observed with trial repetition (exposure to the same open field). Finally, we showed that although overall habituation was found with trial repetition, individuals differed in the way they changed (strength and direction) their ROM with repeated exposures. These changes in ROM covaried negatively with ROM during trial 1: individuals with a high ROM in trial 1 showed quick habituation, whereas individuals with a low ROM showed no change or even sensitization (i.e. increase in ROM).

Consistent individual differences in open field tests have been demonstrated in many taxa (e.g. Boon et al., 2007; Budaev, 1997; Burns, 2008; Dingemanse et al., 2012; Rodríguez-Prieto et al., 2010; Verbeek et al., 1994) and this is the first demonstration in elasmobranchs. This is an important prerequisite for linking captive behavior with field observations, paving the way for more in depth exploration, such as the proximate and ultimate causes of these differences. An important future step is also to investigate consistency and plasticity of individual differences over longer time periods. We tested juvenile sharks and although personality can be long lasting, even across ontogenetic shifts (Wilson & Krause, 2012), personality is not always stable across the life span (Petelle et al., 2013). Overall, our study demonstrates the potential of the open field test for elasmobranchs and hopefully stimulates the use of this method to test and understand consistent individual differences in lemon sharks and other elasmobranchs.

As already noted, behaviors during open field tests can be interpreted differently. We observed a change in ROM with repeated exposures that we ascribe to novelty loss (Dingemanse et al., 2012; Warren & Callaghan, 1976). Therefore, this behavior most likely reflects a reaction to novelty and not solely general activity. Typically, the open field test is thought to measure exploration; however, some authors have interpreted it as a boldness test (Toms et al., 2010). Stress is likely to play a role in any experiment using novelty. For example, less explorative individuals are more likely to be stressed by exposure to the open

field than more explorative ones. In such a scenario, it becomes very challenging to disentangle neophilia and boldness and this might also depend on the species studied (for instance its trophic level associated with the risk perceived from a novel environment). Not only is it unclear how novelty is perceived but also whether individuals habituate to the open field per se. Our open field test encompassed novelty in its shape, and sharks had never visited it before, but the environment did not differ markedly from the holding conditions. Therefore, one might question the strength of the novel environment stimulus and other interpretations should be also considered. First, the observed decrease in ROM could reflect habituation to the ushering and handling in general rather than the novel open field per se. Although we cannot exclude this possibility, we believe that handling stress was minimal: sharks were never directly handled, never entered the start box in an erratic way while being ushered and were given 5 min before entering the test pen by themselves. Second, our results might be due to habituation to being in captivity. However, since time in captivity had no effect on ROM or habituation/sensitization rate we can probably rule out this possibility. Using a habituation/sensitization approach can be instrumental in guiding research in this and other species and has demonstrated that activity in a novel open field is not to be confounded with general activity. Future studies could produce validity tests (e.g. Beckmann & Biro, 2013; Burns, 2008; Carter et al., 2013; Dochtermann & Nelson, 2014) and pinpoint the exact stimuli to which sharks habituate.

Individuals varied in their change in ROM and these changes were negatively correlated with their first ROM scores. These analyses were performed following the logic under the reaction norm framework (Dingemanse et al., 2010); our results suggest that elevation (ROM trial 1) and slope (change in ROM over trials) covary. Behavioral reaction norms are usually analyzed with random slope mixed models (Dingemanse et al., 2010). However, in our case the power was insufficient to allow this approach. Despite this low

power, a strong negative correlation between intercept and slopes was still found. Furthermore, when controlling for personality-related differences in habituation/sensitization, the repeatability estimate increased to 0.51 (from 0.28). Therefore, instead of dismissing individual variation in plasticity, we used a method similar to Rodríguez-Prieto et al. (2010) to obtain estimates of the change in ROM with trial repetition. Doing this, we found a strong negative relation between ROM trial 1 and habituation estimates demonstrating a relationship between personality and plasticity (i.e. habituation/sensitization). This method is less accurate than the random slope models (Martin & Pelletier, 2011) but, in our opinion, the presence of strong individual differences in habituation/sensitization rate which are related to personality cannot be dismissed. Sharks could only be kept for relatively short periods and observation time was constrained by external factors such as tide or light, constraints not uncommon for studies on aquatic megafauna. In such scenarios, it is important to conduct power simulations to avoid dismissing biologically important observations (Martin et al., 2011).

The repeatability estimated over all six trials (0.28) was substantially lower than when controlling for individual differences in plasticity (0.51) or when only the two first trials were included (0.50). Most likely, with increasing exposure the effect of individual differences in plasticity changed the ranks of individuals obtained in the first trial, as further evidenced by the loss of repeatability when only the first and last trials were considered. One alternative explanation might be a reduction of individual variances during habituation. Indeed, the loss of significance when only trials 5 and 6 were considered might indicate this. However, a trend was still apparent comparing trials 5 and 6 and repeatability was close to the repeatability of the first two trials (0.39 versus 0.50). This suggests that rank disturbance was the prime cause for the decrease and loss of repeatability. However, the decrease of variance due to habituation should not be ignored either; exposing sharks more frequently could further investigate this effect. Regardless of the causes, if one is interested in testing reaction before

habituation such as reaction to novelty, our results illustrate the need to acknowledge rank disturbance and general effect of habituation, either using random mixed models if data resolution allows or by limiting the number of trials in the analyses.

Personality-related plasticity differences have been demonstrated in several taxa (Mathot et al., 2012). Interestingly, we found strong differences in the direction of change, with some individuals decreasing, some not changing and others increasing their ROM. Similarly, strong differences between individuals in their habituation/sensitization rate (to a low-risk predator) and a negative correlation between exploration score and these differences were found in Iberian wall lizards, *Podarcis hispanicus* (Rodríguez-Prieto et al., 2010). Furthermore, different inbred strains of mice, *Mus musculus*, varied in their direction of activity change (decrease, increase or no change) with trial repetition (Bolivar et al., 2000) suggesting a genetic effect on the expression of exploration and habituation/sensitization. These studies support our finding, but it has to be noted that the semi-wild conditions of our experimental set-up prevented total experimental control.

An interesting avenue for future investigations is to study the proximate and ultimate causes of this personality-related difference in plasticity. Discussing our results in such a context is premature but empirical and theoretical investigations help direct future research. In the particular case of exploration and habituation/sensitization, insights can be gained from studies on rodents. In these animals, there is evidence for neurochemical, morphological and genetic factors underlying habituation (Leussis & Bolivar, 2006). These studies do not always focus on individual differences but might help explain the proximate causes of our observed effects. For instance, glucose is known to impact habituation in rodents (Leussis & Bolivar, 2006) and, likewise, individual differences have been found in juvenile lemon shark blood glucose during stressful events (Brooks et al., 2011). It would thus be informative to correlate these blood parameters with behavior in a novel open field and habituation/sensitization rate.

Another explanation for the observed variation could be cognitive differences between individuals (Carere & Locurto, 2011; Guillett et al., 2009; Sneddon, 2003). These hypotheses could be further investigated as classical conditioning experiments in this species suggest inter-individual cognitive differences (Gruber & Schneiderman, 1975). Overall, little is known about how such personality-related differences in plasticity (including habituation/sensitization) can be selected and under which environmental conditions. Such causes have, nevertheless, recently been discussed (Dingemanse & Wolf, 2013; Mathot et al., 2012) and their demonstration needs a clear and broad understanding of the study species and study system.

3. Are some sharks more social than others? Short and long-term consistency in the social behavior of juvenile lemon sharks

J.S. Finger, T.L. Guttridge, A.D.M. Wilson, S.H. Gruber & J. Krause

Despite substantial research interest in understanding individual-level consistency in behavioral attributes, significant knowledge gaps remain across traits and taxa. For example, relatively few studies have looked at social personality in large marine species such as elasmobranchs and whether or not individual differences in behavior are maintained in unstable social groups (i.e. fission-fusion dynamics). However, it is important to investigate this topic in other model species than the usually small species with short generation times typically investigated in these areas of behavioral ecology. Indeed, studies on ecologically diverse taxa could provide mechanistic insights into the emergence and maintenance of animal personality and dynamics of social groups in animals. In addition, understanding social behavior at the group- and individual-level could improve conservation management of these large animals with long generation times (e.g. removal of particular behavioral types by fisheries practices). Here, we investigated consistent individual differences in sociability in wild juvenile lemon sharks over both short- (4 to 18 days) and long-term (4 months) sampling periods. Individual sharks were observed in social groups and scored according to the number of social interactions performed during observations. Despite variable individual group compositions between repeated trials, sharks showed consistent individual differences in their social behavior over both time scales. These results suggest reduced plasticity and highlight individuality as an important explanatory variable for the social dynamics of juvenile lemon sharks. In addition, long term stability observed in this wild population demonstrates the importance of personality in the daily behavioral repertoire of juvenile lemon sharks. Our results are discussed in the context of other shark studies and taxonomic groups and potential avenues for future research are proposed.

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INTRODUCTION

Animal personality, consistent individual differences in behavior across time and contexts, has been described in a broad spectrum of taxa (Gosling 2001; Reale et al. 2007; Sih et al. 2004b) and is recognized as a fundamental aspect of ecology and evolution (Sih et al. 2012; Wolf & Weissing 2012). Furthermore, it is now understood that individual differences need to be incorporated within conservation management programs (Conrad et al. 2011; Mittelbach et al. 2014). However, a primary obstacle for many species, including large-bodied marine animals such as sharks, lies in the fact that not enough data exist to understand if and how the inclusion of personality could benefit such programs. This issue can be problematic considering the sensitivity of mega-fauna to anthropogenic harvest and overexploitation (e.g. Estes et al. 2011; Lewison et al. 2004). For example, sharks have only recently received attention from an individual-based behavioral standpoint (e.g. Finger et al. 2017; Huveneers et al. 2013; Matich & Heithaus 2015; Towner et al. 2016; Vaudo et al. 2014) and a behavioral consistency standpoint in the last few years (Byrnes & Brown 2016; Byrnes et al. 2016a, b; Finger et al. 2016; Jacoby et al. 2014; Wilson et al. 2015). In terms of consistency in individual social behavior, what little information there is remains unclear and in need of further study. For example, Jacoby et al. (2014) found consistent individual differences in social network position in a captive population of juvenile catsharks but significance was lost once the group effect was controlled for. In contrast, Wilson et al. 2015 found no evidence of consistency in social network position in wild juvenile lemon sharks.

Sharks are generally large-bodied, long-lived animals with a large brain to body mass ratio (Northcutt 1977; Yopak et al. 2007). They exhibit slow growth and reproduction rates, while occupying a relatively high trophic position (e.g. Dulvy et al. 2014; Stevens et al. 2000). As a result, sharks could be an interesting addition to smaller aquatic vertebrates (with relatively fast generational turn-over) usually studied within the animal personality

framework. For instance, while predation is often a factor underlying the evolution of social grouping, as frequently seen in teleost fishes (Krause & Ruxton 2002), some gregarious shark species such as the scalloped hammerhead (*Sphyrna lewini*; Klimley 1985) actually experience low risk of predation overall. It is then conceivable that alternative selective pressures shaped the evolution of social behavior in many shark species. As similar assumptions could be drawn for individual differences in sociability, it is important to further investigate personality in sharks. In addition, expanding this research to wild populations and long-term observations will help to determine the importance of personality to sharks' everyday life. Because sociability has already been described in different shark species (e.g. Guttridge et al. 2009; Guttridge et al. 2011; Jacoby et al. 2012a; Klimley 1985; Mourier et al. 2012, 2017; Myrberg & Gruber 1974), it is a critical step for the development of better management programs. Indeed, the removal of particular personality types (Biro & Post 2008; Biro & Sampson 2015; Sutter et al. 2012) through fisheries might have unknown consequences for the food web, ecosystems and environmental management. For example, the documented risk posed by fishery targeting aggregations (Jacoby et al. 2012a; Mucientes et al. 2009), could conceivably select against social individuals (i.e. higher tendency to aggregate).

We investigated the presence of consistent individual differences in the social behavior of wild juvenile lemon sharks by testing groups of six individuals. However, this study differs from those previously conducted in several aspects. First this study assessed consistency over both short (4-18 days) and long-term (4 months) periods in wild sharks. Long-term observations have obvious benefits (Stamps & Groothuis 2010) but are rarely conducted on wild animal populations (Archard & Braithwaite 2010) and especially with such long-lived species. However, a major difficulty in generating long-term data sets is that individuals disperse or suffer mortality (Gruber et al. 2001), which can lead to different individuals being caught during a given sampling event. To account for this here, except for a

subset of the data, individuals were haphazardly assigned to groups for retests, leading to variation in individuals' social environments (i.e., group composition). This approach provided the opportunity to determine if observed consistency in tendency to socialize can be attributed to individual differences and is not just a result of group effects and composition (Cote et al. 2012; Harcourt et al. 2009a; Kurvers et al. 2009; Pritchard et al. 2001). In addition, changing group composition while testing social personality in captivity reflected rapid changes in social partners commonly observed in juvenile lemon sharks in the wild (Guttridge et al. 2011; Wilson et al. 2015). Indeed, this aspect (among others) of their social dynamic has been shown to resemble that of wild guppies, a fish species demonstrating social fission-fusion behavior (Wilson et al. 2014, 2015). In summary, we tested the predictions that wild individual juvenile lemon sharks consistently differ in their social behavior over short (5 to 18 days) and long-term (4 months) tests and further, that these differences were robust to changes in group composition.

METHOD

Study site and Sharks

This study was conducted on Bimini (20° - 28°N, 72° - 80°W), situated approximately 85 km east of the coast of Florida (USA) in The Bahamas. Wild juvenile lemon sharks from two adjacent mangrove-fringed habitats (North Sound and Shark Land) were captured using gillnets (see Manire & Gruber 1991 for details) in June (7-day capture session) and November 2012 (3-day capture session). Upon capture, each individual was measured (pre-caudal length: PCL), sexed and equipped with a unique color-coded tag (T-bar type, Floy Tag Manufacturing) for visual identification.

Lemon sharks were our test subject because they are a common, large coastal species in the western Atlantic. In some locations, they show long-term site attachment (approx. three

years) allowing their capture and recapture over extended periods while living in their natural habitat (Chapman et al. 2009; Dibattista et al. 2007; Morrissey & Gruber 1993). In addition, they have been successfully used in semi-captive behavioral experiments (e.g. Guttridge et al. 2009; Finger et al. 2016).

Experimental set-up

Sharks were housed in a large oval-shaped pen (10 x 5 m) constructed just offshore in the North Sound on sand bottom flats. They were given at least four days in the holding pen to acclimatize to captive conditions before beginning the experimental procedure. During holding time, they were fed every three days on a diet of fresh and frozen local fish (*Sphyraena barracuda*).

A channel (length, 4 m) linked the experimental pen to the holding pen. The circular experimental pen (diameter, 10 m) was equipped with a camera recorder placed 6 m above the center and operated by a system of ropes. A wooden tower (height, 3 m) was placed outside the pen to allow observations (Fig. 1).

The day before observation, six sharks, selected to reduce size difference (within PCL ± SD = 4.7 ± 2.73 cm), were ushered into the experimental pen, fed to satiation (to insure similarity of hunger level between individuals) and left overnight to acclimatize to their environment. Sex has been shown to have no influence on social dynamics of juvenile lemon sharks in Bimini (Guttridge et al. 2009, 2011) and was not considered further in the design of this experiment. On the day of observation, the swimming behavior of the six individuals was filmed for 20 minutes. Each individual was marked on their dorsal fins with unique color-coded tags to allow for subsequent identification and tracking during video analyses. Upon completion of filming, sharks were released, or relocated to the holding pen to await further retesting (see below for test periods).

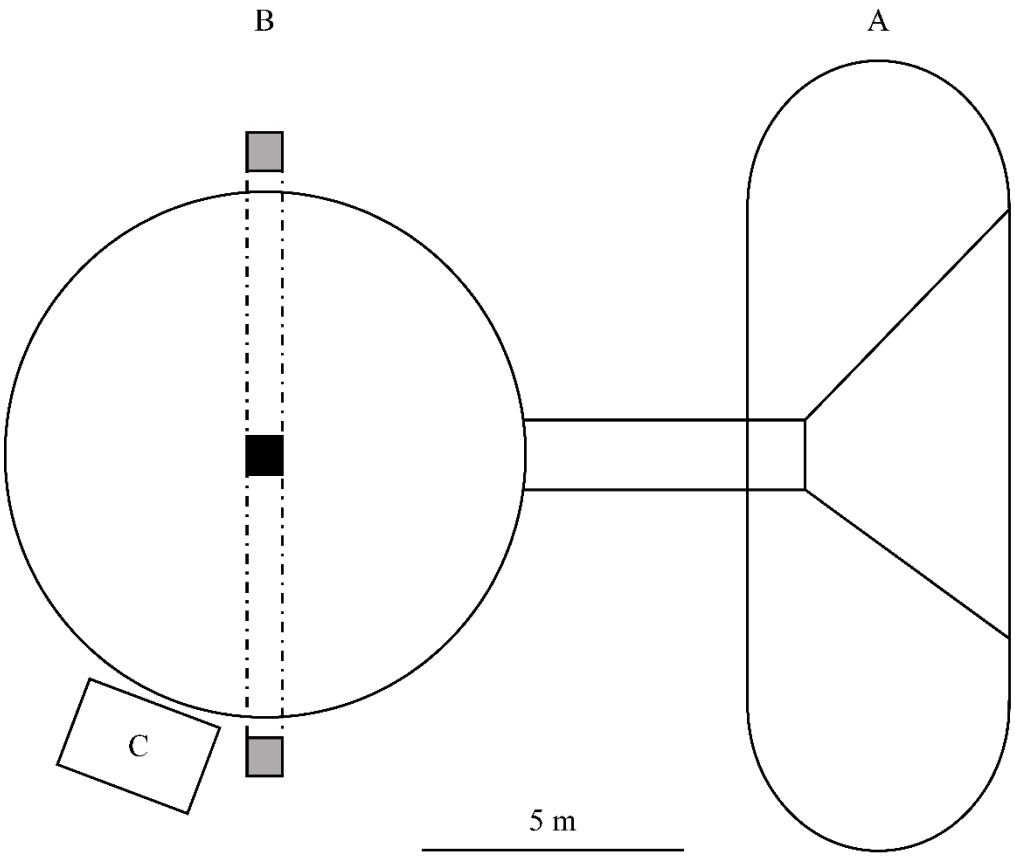

Figure 1: Schematic of the experimental setup in Bimini, Bahamas with holding pen (A) separated into compartments containing size-matched sharks, linked to the experimental pen (B), via channel. On both sides of the social pen, there are two vertical wooden posts (brown squares) linked by ropes (dashed lines) used to raise and slide the camera (black box) above the center of the experimental pen. Identification of individuals and camera operation are performed from a wooden tower (C).

Test periods and group composition changes

During this study, two rounds of tests were carried out: June and November 2012. In June, individuals were tested only once (N=84; 41 females and 43 males, mean pre-caudal length ± SD = 51.8 ± 5.7 cm) and then released in their natural habitat. In November, all sharks (N=48; 19 females and 29 males, mean pre-caudal length ± SD = 54.3 ± 6.1 cm) were tested twice (time between tests: 4 to 18 days; 8.5 ± 4.3 days), and of these individuals, 23 (14 females and

9 males) had been tested in June previously. Each observation session started at similar water depth (mean depth ± SD = 79 ± 12.4 cm), 1.5 hr before or after a slack low tide.

Group composition changes occurred haphazardly between June and November tests (23 individuals from 11 different groups from June were haphazardly allocated to 8 groups in November). Group mixing between test and retests in November consisted of exchanging half of a group (3 individuals) with another half. Such mixing occurred for 4 groups (N=24 individuals) whereas for 4 other groups composition remained unchanged.

Social interaction observations

During video processing, data were recorded every 30 seconds, across 20-minute observation sessions (thus 40 observations in total); each time the focal individual was recorded as social or asocial. Juvenile lemon shark social behavior is characteristically composed of following or paralleling with other individuals (see Table 1 for definitions). A leading event can be defined as occurring when one individual is being followed but is not paralleling or following another individual (Table 1). As a focal individual being followed might not reflect its wish to socialize, we considered only "active" events of social interaction (i.e. following and paralleling) as a social interaction performed by this individual. Resting and milling (see Table 1) were designated here as non-social events for two reasons. First, resting behavior in juvenile lemon sharks is not well understood and it has been shown that most (>95%) social interactions occur during active swimming (Guttridge et al. 2009). Second, individuals were considered as social only when being notably influenced by another individual. Two (or more) individuals could cross paths but if neither of them modified their swimming movements then they were not considered to be interacting. Each individual's social behavior score was obtained by summing the number of active social events (see below) over the 40 observations. All sharks in the arena were observed in this manner.

Table 1 Social behavior of juvenile lemon sharks. Each of these behaviors is only considered when individuals are within 2.5 body lengths of each other. Table modified from Guttridge et al. (2011).

Behavioral State	Definition	Included as social score
Following	An individual mimics trajectory of followed individual.	Yes
Paralleling	Individuals swimming side by side either at similar speed or while overtaking/being overtaken.	Yes
Milling	Individuals swimming in a non-coordinated manner.	No
Leading	Being followed but not paralleling or following another individual.	No

An algorithm was developed to quantify the social behaviors described above. This tool has also been used to analyze juvenile lemon sharks' social behavior in another study (Keller et al. 2017). Briefly, for each of the 40 observations, this algorithm used position (coordinates of the tip of the snout) and orientation of the six individuals at time *t*, *t*+1 and *t*+2 second. Orientation was obtained relative to the previous point, therefore, at time t, orientation was obtained by adding a tracking point at t-1 second. Tracking was completed manually by marking the snout of each shark using MtrackJ (Meijering et al. 2012) within ImageJ (Rasband 1997). Using these data, the algorithm calculated distances between individuals, along with the differences in orientation and position (front, behind, side by side) between sharks. Additional tracking (t+1 and t+2 seconds) was used to determine if overtaking occurred, and if a dramatic turn of one shark (creating a large orientation difference at time t) influenced (i.e. following) other individuals (resulting in similar dramatic orientation change of the followers during t+1 and t+2). The resulting values obtained from these calculations

allowed the algorithm to define each individual's social behavior as following (within social distance and behind another individual and similar orientation or influenced by this same individual), paralleling (within social distance and side by side or overtaking another individual and similar orientation than this same individual) or asocial (outside of social distance or not being influenced by other individuals). Upon completion, the algorithm provided the total number of social events over the 40 observations (paralleling and following; Table 1) as the individual social score in this investigation. The use of videos and this algorithm to record and analyze behavioral data, greatly reduced any potential observer bias.

Social distance

Previous studies used a maximum social distance of either one (Wilson et al. 2015) or four body lengths (Guttridge et al. 2011) when considering social interactions of juvenile lemon sharks in semi-wild or wild conditions. In contrast, 2.5 body lengths between individuals were found to be best in our experimental setup. This value was observed as being the maximum distance at which individuals performed following behavior during preliminary video analyses (distance was calculated using coordinates of sharks in videos and absence or presence of social interaction was determined by two observers).

A comparison between social distances (i.e. 1, 2.5 and 4 body lengths) showed that below 2.5 body lengths, a large number of associations were missed but above 2.5 body lengths only very few were added.

Algorithm reliability

To control for the reliability of this algorithm, 4 videos that were processed through the algorithm were also analyzed manually. Observers, naïve to the algorithm, were asked to describe each individual social behavior as describe above (to mimic analyses by the

algorithm). Social scores obtained from manual observations and the above algorithm were highly correlated (Spearman's rank correlation: $r_s = 0.96$, N=24, P<0.001) and did not differ significantly (Wilcoxon paired test: V=138.5, P=0.71, N=24). We therefore concluded that the algorithm showed results highly similar to those obtained through manual observation and could therefore be confidently applied to the full data set.

Short and long-term tests

To test short-term consistency, analyses were performed within the November period overall, then we divided this period into groups of mixed and non-mixed composition. To test long-term consistency, analyses were performed between observations from June and November. We took the first trial of November tests instead of the average between the two trials to minimize the potential of confounding effects (due to habituation, familiarity development etc.).

Correlation and permutations

To investigate consistent individual differences in social behavior, we first used Spearman rank correlation analyses within the different subsets of data described above. If a significant correlation was found (for short-term or long-term data) a permutation analysis was performed. For permutation analyses, individual social scores were randomly sampled from the social groups they were tested in. Therefore, a shark could be assigned only a social score from another shark (or his own) from the same social group. This was applied to June, November first and November second trials. Using this randomly permuted data, correlation tests were performed between trials (e.g. correlation between permutated June and permutated November first trial for long-term tests) and the Spearman's rho estimations extracted. This step was repeated 10,000 times to obtain a distribution of randomly simulated rho for each correlation we were interested in. This distribution was then compared to the observed rho

(estimated from original data) by extracting the proportion of simulated rho greater than the observed rho (thereafter referred to as P). If P was found to be smaller or equal to 0.025, we deemed our observed correlation significant which was used as a demonstration of consistent individual differences. These within-group permutations were necessary to control for a potential effect of pseudo-replication created by testing individuals in groups (Croft et al. 2011) and the possibility that any observed consistency could be due to consistent differences in overall group behavior between trials.

Repeatability

To provide a repeatability score of sociability along with a 95% confidence interval, the full data set (all trials included) was analyzed using a linear mixed model with individual ID as random factor and sex, size, capture location (i.e. nursery), time in pen before trial and period of observation (June; November) as fixed effects. Social score was normalized using a square root transformation. Normalization of the data allowed the use of the function exactRLRT from the RLRsim package (Scheipl et al. 2008) to test significance of the random term (i.e. individual ID). Repeatability was calculated according to Nakagawa and Schielzeth (2010). The 95% confidence interval was calculated using the confint function from lme4 package (Bates et al. 2015). These analyses were performed on the overall data set. All analyses were performed in R v3.2.3 (R Core Team 2015).

RESULTS

Consistency in social behavior was found over short-term periods of several days (Spearman rank correlation: r_s=0.43, N=48, P<0.001, Fig. 2a) and long-term periods of four months (Spearman rank correlation: r_s=0.52, N=23, P = 0.01, Fig. 2b). The consistency found here was not caused by differences in overall group behavior (permutation analyses: short-term tests: P=0.005; long-term tests: P=0.0088).

Within short tests, those that did not experience any changes in group composition did not show consistent differences in social behavior (Spearman rank correlation: r_s=0.39, N=24, P=0.057,) whereas individuals that experienced a mixing of groups did (Spearman rank correlation: r_s=0.43, N=24, P<0.05; Permutation analyses: P=0.0094). However, individuals from the short-term non-mixed group showed consistent individual differences as well, when one outlier (see Fig. 3a) was removed (Spearman rank correlation: r_s=0.58, N=23, P<0.01).

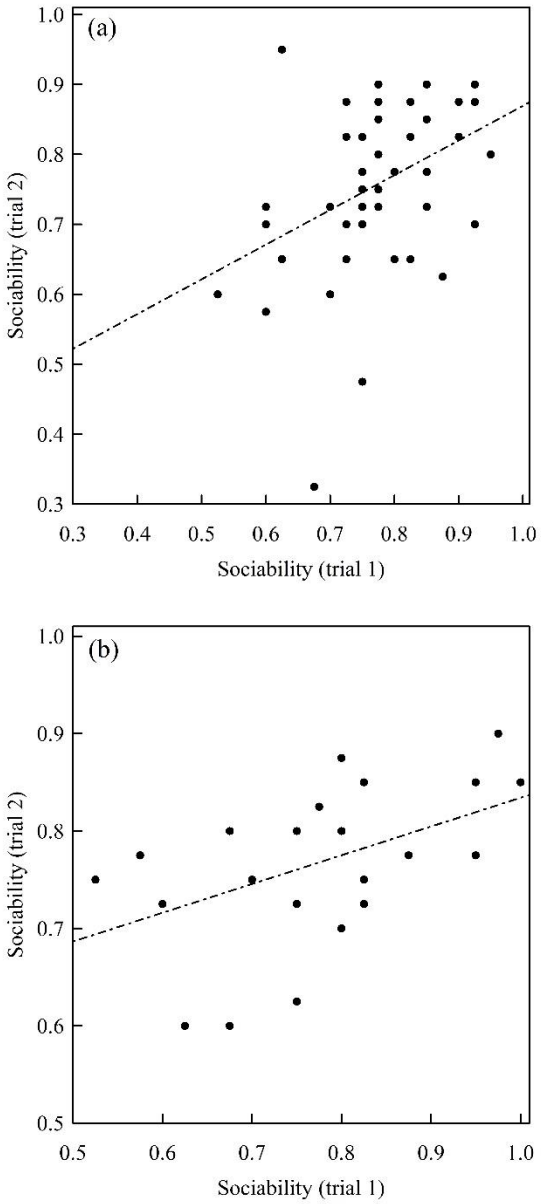

Figure 2: Comparison of sociability score for juvenile lemon sharks in Bimini, Bahamas between trial 1 and trial 2 for short-term (a) and long-term (b) test retests.

Overall, juvenile lemon sharks demonstrated repeatability in their social behavior (repeatability= 0.49; CI: [0.36, 0.51]; RLRT=16.578, P<0.001) when controlling for size, sex, location of capture, time in captivity before observations and period of testing.

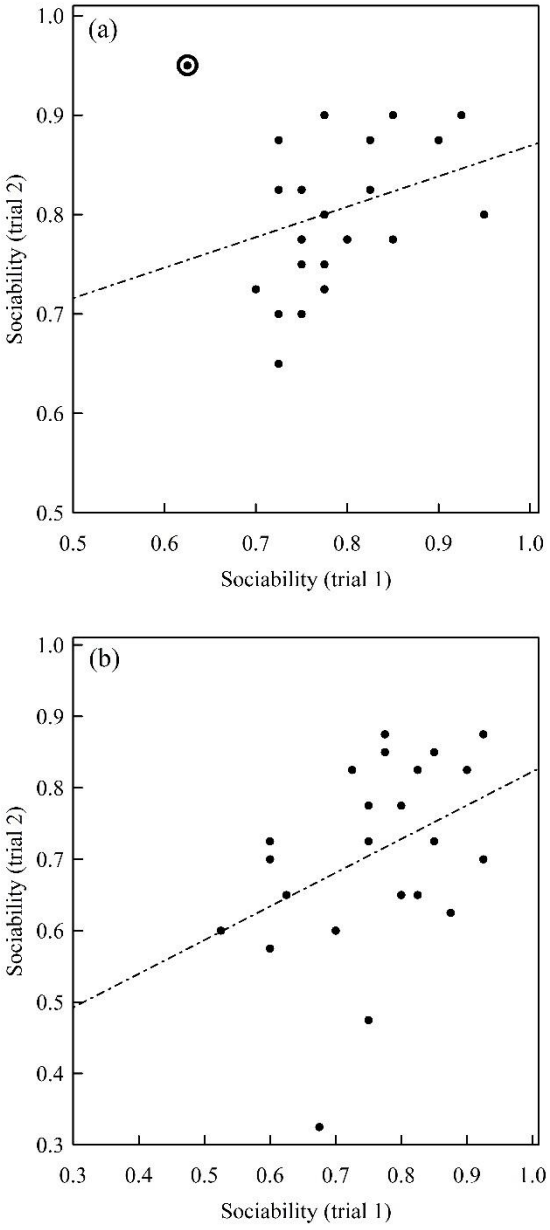

Figure 3: Comparison of sociability scores between trial 1 and trial 2 for short-term showing individual juvenile lemon sharks (Bimini, Bahamas) that experienced no change (a) and change (b) in group composition between test and retests. The circle identifies a potential outlier mentioned in the text above.

DISCUSSION

In this study, we explored the presence of a social personality trait in wild juvenile lemon sharks. In doing so we found that sharks consistently differed from each other in some aspects of their social behavior despite being tested in groups (see Webster & Ward 2011 for mechanisms having the potential to suppress individual differences) over a four-month period. Overall, we found a repeatability of 0.49, which is relatively high (see Bell et al. 2009) and consistent with other studies of wild populations (Bell et al. 2009). In addition, consistent individual differences were still maintained despite changes in group composition. The later result indicates that, at least in the juvenile lemon shark population studied, individual social behavioral types play an important part in the social dynamics of these animals and could have a strong impact on their social behavior in the wild.

As mentioned above, social personality has already been investigated in sharks (Jacoby et al. 2014; Wilson et al. 2015). However, our study differs from these other investigations in several important points. First, despite using the same species and age criterion, Wilson et al. (2015) did not find consistency in the social proxies they used. While these contrasting results might be attributed to dissimilarities between populations, there are also several methodological discrepancies between Wilson et al.'s study and ours (e.g. sampling method/frequency and smaller sample size). A convergence of methods, to investigate consistent individual differences in these two juvenile lemon shark populations would be useful. Indeed, the possibility to compare between populations might lead to important insights into causes of emergence and maintenance of animal personality. Second our investigation differs from Jacoby et al.'s (2014) study in which consistent individual differences in the social behavior of juvenile catsharks were detected. While they maintained the composition of social groups in their experiments, we allowed it to vary between trials in ours. This was an important aspect of our experimental design for two reasons. First, we believe that our approach reflects natural social mixing between individuals likely to occur in

juvenile lemon shark nurseries. Second it indicated that our observed results were not caused by consistent overall group differences. Similarly, keeping group composition constant between trials to investigate social personality in the catshark (Jacoby et al. 2014) may blur the distinction between individual and group behavior differences as causes for Jacoby et al's observation. This concern is reinforced by the fact that individual catsharks prefer certain individuals over others (Jacoby et al. 2012b) which might influence individual social tendency based on group composition. However, in contrast to juvenile lemon sharks, in catsharks not mixing group composition and allowing affinity to develop reflects their ecology during early life stages. Indeed, they are a sedentary species that hatch in egg clusters, display high site fidelity and are therefore expected to have a pre-determined and relatively stable social environment (D.M.P. Jacoby personal communication). Therefore, mixing group composition in this system might not be relevant to describe the social dynamic of juvenile catsharks in the wild. This highlights the importance to carefully consider the ecology and natural behavior of the species if one is interested in understanding the consequences of individual differences in behavior in the wild. Nevertheless, the contrast between these two species provides interesting systems to investigate social dynamics in two alternative social systems. Here again, converging methods in future work could be highly beneficial in our understanding of animal personality and social systems in animals. This overall illustrates an unexpected diversity in shark social systems that could provide interesting data if further studied.

Cote et al. (2012) gave individual mosquitofish (*Gambusia affinis*) a choice between shoals of different sizes and compositions in binary choice experiments and found that despite an effect of these two characteristics, individual differences in sociability were still detectable. Even though our investigation differs in several ways including the choice to let individuals interact together, our results are in agreement with the maintenance of individual differences despite social context changes. It is important to note a relative similarity of what is

considered as a social interaction. Indeed, in a binary choice experiment, observers record only "active" attempts of socializing from the focal individual. Similarly, in our experiment, we recorded a behavior as social only when the focal individual actively interacted. Being followed by another individual was not considered as social which led to classify leading as asocial, in contrast to the commonly used gambit of the group, for instance. We believe that this treatment of leading events could be related to the distinction between effective (an individual able to impose its preferences) and intrinsic leaders (the tendency of an individual to pursue its own preference) discussed by Johnston and Manica (2011). However, instead of imposing other individuals to follow, it seems that an intrinsic leader becomes an effective leader only in the presence of followers. This, in turn, suggests that some aspects of individual behavior are relatively fixed even in groups and could play an important part in the dynamic of social groups (Harcourt et al. 2009b; Laskowski & Bell 2014). However, further tests are needed to investigate this hypothesis in juvenile lemon sharks. It could, for instance, be done by experimentally changing group compositions based on known social personality types and observe how cohesion is impacted (e.g. social network measures and group size), especially in an "extreme" social environment (e.g. only asocial individuals). Continuing this work to understand the influence of individuality on social group dynamic is important as it remains poorly studied. Results from the literature indicate that this is dependent on context and/or species (e.g. Brown & Irving 2014; Castanheira et al. 2013; Magnhagen 2012; Magnhagen & Bunnefeld 2009; Magnhagen & Staffan 2005). For instance, Magnhagen and Staffan (2005) found that in perch (*Perca fluviatilis*) the boldness score of individual young of the year perch was strongly modified by other group members. On the other hand, Magnhagen and Bunnefeld (2009) found that in 1-year-old perch individual boldness was also expressed while tested in groups. Interestingly, Magnhagen (2012) suggested that the maintenance of individuality in perch social groups might depend on the experience of predation.

Unfortunately, most of the experiments focusing on personality in a social context tested other personality axes than sociability (e.g. boldness or exploration). A direct comparison with our study is therefore difficult but these differences between investigations are interesting. If further studied in Teleost fishes and sharks, comparative work could lead to a better understanding of overall social group behavior in animals (Farine et al. 2015; Wolf & Krause 2014) while emphasizing the importance of behavioral type into group dynamics.

Contrary to expectation, individuals that experienced the same group composition between tests showed a lack of consistency. A potential explanation would be an unforeseen familiarity development during the experimental procedure. This has been demonstrated to influence social interactions in this species (Keller et al. 2017) and in catsharks (Jacoby et al. 2012b). A simpler explanation might, however, be the influence of one outlier and indeed once removed consistency was found.

Long-term stability of personality traits has been described in other animals (Beleyur et al. 2015; Debeffe et al. 2015; Koski 2011a; Wuerz & Kruger 2015) including fish (Boulton et al. 2014; Castanheira et al. 2016; King et al. 2013; Vrtelova et al. 2016). However, only a few studies have demonstrated long-term consistency of social behavior in wild populations (see for instance: Aplin et al. 2015; Cote & Clobert 2007), as shown here in juvenile lemon sharks. These are interesting results when contrasted with a study by Nakayama et al. (2013), describing that the individual tendency to follow is experimentally changeable (i.e. using reward) in the three-spined stickleback. If the tendency to follow is plastic and can change depending on experience, one can ask how individual differences are maintained over a long period in the wild (e.g. positive feed-back loop, highly stable environments). Trying to experimentally modify the tendency to follow in juvenile lemon sharks would be an interesting first step in this direction. The demonstration of such long-term consistency is also ecologically important. Indeed, even if a four-month period is relatively short compared to the

age of maturity in this species (sexual maturity is reached at 12 years old; Brown & Gruber 1988), the first three years of life (ontogenetic stages of this investigation) represent a critical life-history period for juvenile lemon sharks, due to their high natural mortality (Gruber et al. 2001; Dibattista et al. 2007). Finding individual behavioral consistency during this period suggests that personality could have an impact on everyday life of juvenile lemon sharks. One logical next step would be to investigate the ecological consequences of long-term consistency in juvenile lemon sharks. Nevertheless, longer term tests are still required to confidently conclude that individual differences are indeed stable over the entire three-year period during this life stage. Such long-term studies are overall rare and absent for elasmobranchs. It is, therefore, important to extend such research to further populations and species to better understand stability and the ecological consequences of personality in these animals. This would overall benefit the study of animal personality by giving insights into the emergence and maintenance of individual differences (e.g. Bergmuller & Taborsky 2010; Dingemanse and Wolf 2010; Dall et al. 2004; Stamps 2007; Wolf et al. 2007).

Overall, this study has shown that individual juvenile lemon sharks vary in their tendency to socialize in a consistent manner. Consistency was maintained despite changes in group composition. These results indicate a potential strong impact of individuality on group behavior. It could be rewarding to extend this approach to other taxa and investigate in which circumstances consistency takes over plasticity in the tendency to socialize. Furthermore, the fact that these variations between individuals persist through relatively long-time periods suggests that personality is an important aspect of sharks' behavior that could have both ecological and evolutionary impacts. Finally, these results show that the behavioral complexity of sharks (and other elasmobranchs) is underestimated and that this taxonomic group deserves more attention.

4. Behavioral syndrome variation in a population of wild juvenile lemon sharks

J.S. Finger

Following the demonstration of behavioral syndromes in animals came the realization of variation in these correlations between population and species. Such variation could be used to understand the emergence and maintenance of personality in animals. However, it requires both a diversity of taxa tested and the development of wild population models to identify natural causes of such variations in correlations. These points have generally been overlooked. Indeed, as empirical evidence and animal models are accumulating in captive environments, only a few studies have attempted to look at behavioral syndrome variation in wild populations of large animals. This chapter contributes to fill this gap by investigating the presence of a syndrome between exploration and sociability in a population of wild juvenile lemon sharks. Due to the possible environmental and ontogenetic variation in syndromes, the population was separated by nursery and age class. I found a negative correlation between exploration and sociability in sharks aged from 1 to 3 years old but only from one nursery. It is not clear if an opposite (positive) or no syndrome is present in sharks from the other nursery. In addition, I did not detect any syndrome or consistency in young of the year sharks. These results illustrate the importance to consider both development and environmental differences while investigating behavioral syndromes in the wild. This investigation also highlights the juvenile lemon shark as an interesting model for the study of the emergence and maintenance of animal personality.

INTRODUCTION

It has been demonstrated numerous times that animals from the same population can demonstrate marked individual differences in their behavior and that such differences remain consistent through time and/or contexts. This is generally termed animal personality and has been shown to occur in many behaviors throughout the animal kingdom (Bell et al., 2009; Gosling, 2001; Réale et al., 2007). In addition to differences in particular behaviors (that I will refer to as personality axes thereafter) such as predator inspection or reaction to novel stimuli, animals can also show the same individual differences across behaviors. For instance, it has been demonstrated that bolder individuals are usually more aggressive than shy ones (e.g., Huntingford, 1976; Johnson & Sih, 2005). This covariance between behaviors is called a behavioral syndrome (BS) and has been demonstrated in many taxa (Garamszegi et al., 2013; Sih & Bell, 2008), with potential impacts on both the evolution of behaviors and ecology of animals (Conrad et al., 2011; Dochtermann & Dingemanse, 2013; Réale et al., 2010; Sih et al., 2004a; Sih et al., 2012). However, recent studies indicate that BS can vary between populations of the same species instead of an overall common organization of correlated behavior (Bell, 2005; Bell & Sih, 2007; Garamszegi et al., 2013; Urszán et al., 2015 but see Pruitt et al., 2010). This variation has led to exciting areas of research attempting to identify and understand mechanisms and environmental factors developing and/or maintaining such correlations.

Predation risk has received a lot of attention as a biotic factor responsible for the development and maintenance of BS. For instance, in the three-spined stickleback, a BS was present only when predators were present (Dingemanse et al., 2007). In the same species, Bell and Sih (2007) showed that exposure to predation generated a BS in captivity. Another study on the agile frog (*Rana dalmatina*), showed how perceived risk of predation is necessary for ontogenetic development of both consistent individual differences and BS (Urszan et al.,

2015). In addition, emergence of a syndrome between aggression, activity and novelty approach was observed in the first few months of wild brown trout (*Salmo trutta;* Adriaenssens & Johnsson, 2013). Interestingly, the authors suggested that both natural selection and behavioral plasticity were causes for BS emergence. Taken together these studies demonstrate how important it is to consider environmental heterogeneity (here environment is defined as the overall surrounding or conditions in which the animal lives or operates) and ontogenetic development while investigating BS in a population. Therefore, ignoring these potential causes of variation in behavioral correlation represents a risk to disregard or underestimate covariance between behaviors. Furthermore, focused research on these mechanisms responsible for the emergence and maintenance of BS would prove rewarding. For instance, exploring the impact of different environmental components (through development and natural selection) on different personality axes and their correlations across species could enable researchers to identify common mechanisms. However, to do this is important to expand studies on wild populations (Adriaenssens & Johnsson, 2013) and the taxonomical and ecological diversity of species tested (Archard & Braithwaite, 2010; Dochtermann & Dingemanse, 2013; Réale et al., 2010).

One animal group that has been argued to deserve more attention in the field of animal personality are sharks (Finger et al., 2016, general introduction and discussion of this thesis). Indeed, in this group, the study of behavioral syndromes (or even personality) has received little attention. To our knowledge, the first and only investigation of correlation between behaviors was performed in the Port Jackson shark (Byrnes & Brown, 2016). In this species, they found refuging behavior and stress after handling to co-vary. It is however difficult to generalize the presence of behavioral syndromes in sharks with one species. This lack of data is unfortunate as sharks can represent an interesting alternative to most of the aquatic organisms studied to date (see **chapter 1**). The interest is particularly striking because of the

rapid decrease of predation risk throughout ontogeny as opposed to many aquatic species used in personality studies. Therefore, mechanisms responsible for the different aspects of syndromes (e.g. direction, strength, presence, absence) in large (or juvenile stage of large) elasmobranchs might differ from other aquatic species where predation risk remains high throughout their life. Therefore, investigating behavioral syndromes and developing elasmobranchs species models could prove highly rewarding to the field of animal personality.

I investigated behavioral syndromes in the juvenile lemon sharks of Bimini, Bahamas as I believe that its ecology could advance the field of animal personality. Indeed, two personality traits thought to represent ecologically relevant behaviors have been demonstrated in the juvenile lemon sharks of Bimini: activity in a novel open field (mentioned as exploration thereafter; **chapter 2**; Finger et al., 2016) and sociability (**chapter 3**), which provide the opportunity to test for a correlation between these traits. In addition, these sharks are known to have a small home range (0.23-1.26 km²; 5% of available shore line) for the first three years of their life (Morrissey & Gruber, 1993b), spending much of their time near shore and in shallow, accessible water (Guttridge et al. 2012). This allows for long-term, repeatable investigations from newborn to 3-years old sharks providing an opportunity to look at ontogenetic changes. Long-term site attachment also means that individuals will be dependent on the environmental conditions surrounding them. For instance, one population is known to occupy two adjacent nurseries: Sharkland (SL) and North Sound (NS) nurseries (Figure 1). These nurseries differ in their topography with NS being an enclosed area and SL being an open lagoon (Gruber et al., 2001). This difference could be expected to produce biotic and abiotic differences in the sharks' environment. For instance, there is evidence for a difference in predator density between these two nurseries, with SL being riskier than NS (Guttridge et al., 2012; Kessel et al., 2013). Even if the nature and extent of differences is unclear, I believe

that ignoring it could lead researchers to miss BS and therefore discard interesting study systems that could be further developed in the future. Accordingly, instead of studying individuals as a homogeneous population, I classified individuals either as coming from SL or NS and either as young of the year (YOY) or older sharks (OS: from one to three years old). I then tested for the presence of a syndrome between exploration and sociability in these different individual categories. Therefore, I asked if a syndrome was present in OS sharks from SL, OS sharks from NS, YOY sharks from OS and YOY sharks from NS. Then I also investigated long-term consistency in each of the individual categories mentioned above to preliminarily investigate the ontogenetic variations observed in BS (see results).

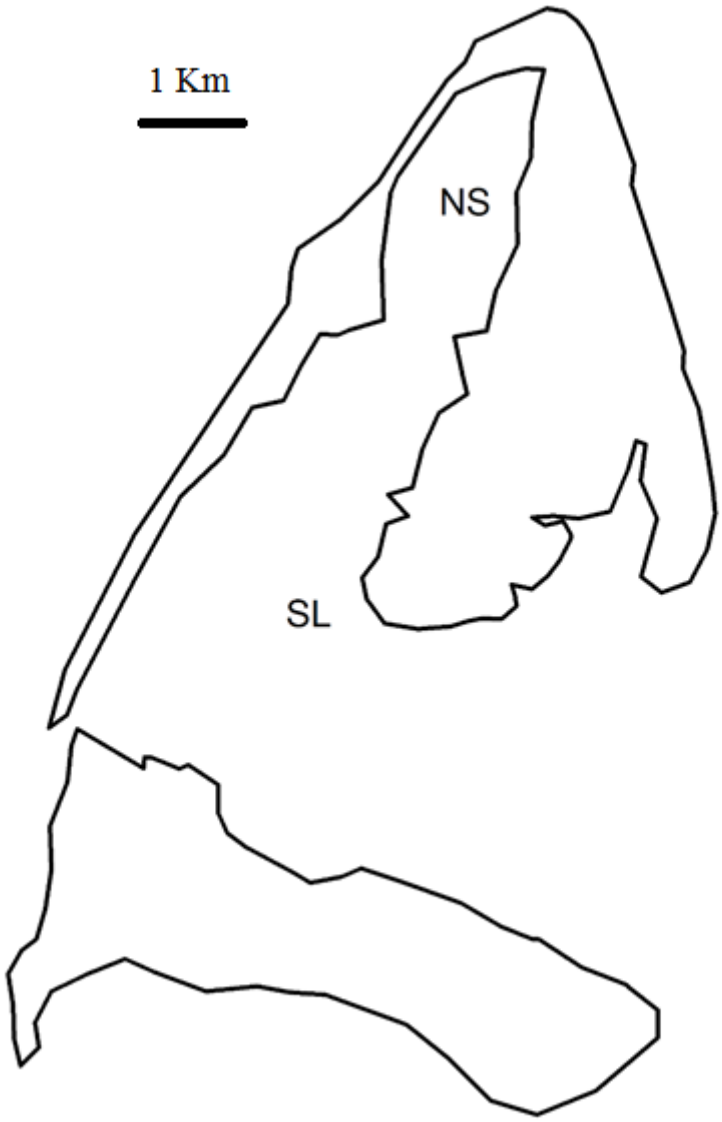

Figure 1: Contour map of Bimini, Bahamas. NS: North Sound Nursery, SL: Sharkland nursery

MATERIAL AND METHODS

Location and Study Animals

This study was conducted in Bimini (20° - 28°N, 72° - 80°W), Bahamas, a chain of islands situated approximately 85 km east of the coast of Florida (USA). Juvenile lemon sharks were captured using gillnets (see Manire & Gruber, 1991 for details) either from the North Sound nursery or Sharkland nursery (Figure 1). Upon capture, each individual was measured for body size (pre-caudal length: PCL), sexed and equipped with a unique colour-coded tag (T-bar type, Floy Tag Manufacturing) for visual identification during observation. New captures were injected with a passive integrated transponder (PIT tag) for identification in subsequent recapture. They were also checked for the openness stage of their umbilical scar. An open umbilical scar would indicate a neonate shark (Dibattista et al., 2007). A new capture (without PIT tag) with a closed umbilical scar was not considered new born as it could have been missed the precedent years. Sharks were housed in a large oval shaped holding pen (10 x 5 m, Figure 2) constructed just offshore in shallow (<1.5 m) sand bottom flats (Guttridge et al., 2009). The holding pen was divided into three compartments containing individuals of different size categories (45-50 cm and <60 cm; 50-55 cm; 55-60 cm PCL). This separation allowed the selection of size matched individuals for social observations.

Sharks were given a minimum of four days in the holding pen to acclimatize to captive conditions before observation started. During non-experimental periods, sharks were fed every three days on a diet of fresh and frozen local fish (e.g. *Sphyraena barracuda*). Sharks were never kept for more than 30-days in captivity.

Experimental protocol

Six juvenile lemon sharks (size-matched, +/- 5 cm PCL) were tested for sociability and activity in a novel open-field in one day. This was accomplished by guiding sharks to

experimental pens (first social pen then exploration pen) through a system of manually operated doors and channels (Figure 2). Observation towers were placed north of the social and exploration pens to facilitate observations and data collections (see Figure 2). A minimum of 8 hours prior to testing, sharks were ushered from their holding pen to the social pen (diameter: 10m) through a channel (length, 4m). They were fed to satiation and left overnight to acclimatize. Observations started the following day, 1.5 hours before or after low tide. This timing assured a depth low enough for video quality (see below) and to avoid long inactive periods (sharks resting at the bottom) that occurs right around or during low tide (personal observation).

Fifteen minutes before data recording, observers positioned a camera to record the lemon sharks' social behavior above the social pen. The sharks were filmed for 20 minutes and videos were processed in the laboratory (see **chapter 3** for details on post processing). On completion, sharks were then observed, individually in the novel-open-field trial. They were selected haphazardly and ushered into a start box (1.5 m half circular pen) for 5 min to then be observed in the novel-open-field for 10 minutes following the method described in **chapter 2**. All six sharks were observed in the novel-open-field on the same day. At the end of each observation, the shark was captured and either released or placed back in the holding pen awaiting further testing. Detailed methods are given in **chapters 2 and 3**. Sociability was measured as the number of times the focal individual was recorded interacting (i.e. Table 1 in **chapter 3**) over 40 observations (e.g. every 30 seconds for 20 minutes), and reaction to a novel-open-field (thereafter mentioned as exploration) was quantified by recording the total number of areas (2x2 meters squares delineated on the floor of the open field) crossed over 10 minutes (Figure 1, **chapter 2**). For the latter measure, multiple visits to the same area were included.

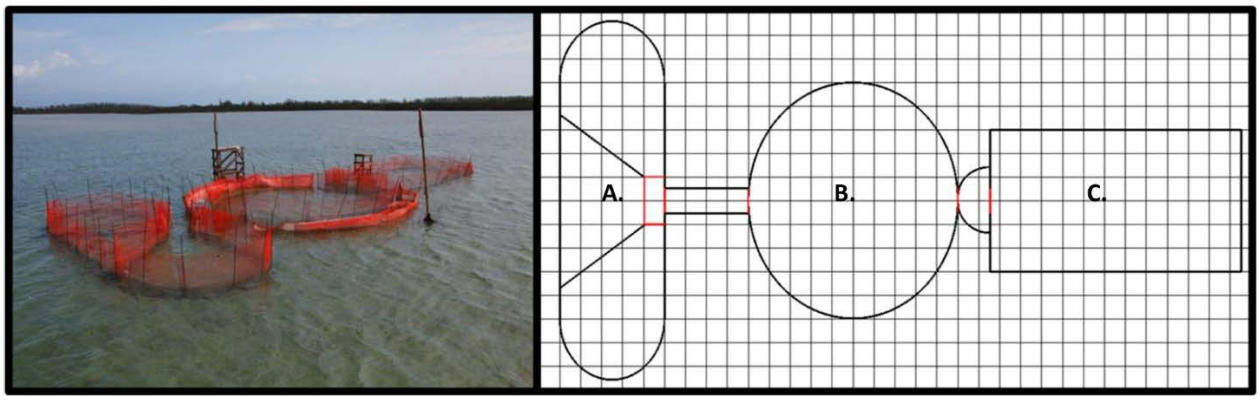

Figure 2: Experimental pens. A. Holding pen, B. Social pen, C. Novel open field. Each square is 1 meter.

Data set

Captures and observations were performed over multiple periods: June-July 2012, 2014 and 2015; March-April 2013 and 2014 and November 2012. Captures also occurred in June 2013 but sharks were released before observation due to an incoming tropical storm. Because of juvenile lemon sharks' tendency to move out of their nursery grounds after 3 years, only individuals between 0 and 3 years old were tested. If age was unknown, only individuals under 66.7 cm PCL were observed. 66.7 cm is the average size found for 3 years old sharks in SL (Barker et al., 2005). In some instances, upon processing of videos, the weather conditions (e.g. high wind) would make reading very difficult. These videos were not included in the analyses. In addition, videos in which at least two individuals were found to wall lean regularly were removed. This was done to prevent risk of mixing up individual identities (i.e. individuals crossing, while wall leaning, were difficult to tell apart). Furthermore, this behavior might be representative of stress (thigmotaxis: Maximino et al., 2010; Simon et al., 1994) which further argues against analyzing these videos. In addition, two videos were removed from analyses because of a high proportion of resting behavior (higher than 35 percent of average resting). Such long periods of rest for many individuals reduced their ability to socially interact which impacted their social score. Finally, observations from open-

field trials were removed if they were interrupted by weather conditions (e.g. thunderstorms). Throughout, the different periods individuals were captured and tested multiple times to evaluate repeatability of both behavioral axes and covariance between these two traits. However, to reduce the potential effect of habituation, I analyzed only up to the first three trials for every individual. For clarity and to facilitate comparison, data removed from one behavior were removed from the other. All the following analyses were performed on this data set. As mentioned in the introduction, this data set was divided into four categories: young of the year sharks from Sharkland and North Sound (YOY SL and YOY NS) and sharks of 1 to 3 years old from Sharkland and North Sound (OS SL and OS NS). Sample sizes are detailed in tables 1, 2 and 3.

Data analyses

Despite being tested in groups of six individuals for sociability, I treated individual scores as independent data in the following analyses. This should not influence the results in a dramatic way as it has been demonstrated that individual differences in sociability are maintained despite group composition changes (**chapter 3**).

To test for the presence of a phenotypic correlation between sociability and exploration, Spearman's rank correlations were performed between these two scores for each individual. Only the first test was used for these analyses as this represents the most representative measure of reaction to novelty (i.e. without habituation effect; **chapter 2**). If a significant correlation was found a partial correlation that controlled for size as a potential confounding effect was then performed using the ppcor package (Kim, 2015). Size was considered as a potential strong confounding factor due to its impact on social behavior (Guttridge et al., 2011) and on exploration (**Chapter 2**). Such an effect could be particularly marked as experimental pens' size did not increase with the size of individuals tested. Sex

was not controlled for because previous studies have shown no effect on either social interaction or exploration in this location (**Chapter 2 and 3**; Guttridge et al., 2011).

To estimate repeatability and covariance between behavioral axes, mixed model analyses were performed. For these analyses, both behaviors were normalized using square root transformations. As previously mentioned, only up to the first three trials for all individuals were used for analyses. Keeping two repetitions per individual (instead of 3) would be the best option to avoid the habituation effect describe in chapter 2. However, it was shown that to detect a syndrome, a large sample size is needed when using only 2 trials per individuals (i.e. more than 200 individuals) as informed by power simulations conducted by Dingemanse and Dochtermann (2013). Because, I did not have this sample size when analyzing age classes and nurseries separately, I choose to include the third trial.

Co-variance between sociability and exploration was analyzed for both nurseries within the two age classes, using a multi-response mixed model (MCMCglmm, Hadfield, 2010). The first model was built with individual identity as a random term, exploration and social score as response variable and size, period of test and trial number as fixed effect. No p-values were given but a 95 % confident interval; I regarded our correlation estimates as significant if this interval did not overlap with 0. The second model was similar to the first one except that sharks' size was removed from the analyses. Each model was run for 700000 iterations with 5000 iterations burn-ins and thinning intervals of 500, three times to confirm stability of results. Prior specification was equivalent to an inverse gamma prior with shape and scale equal to 0.001.

To estimate repeatability of behavioral traits and its significance, each trait was analyzed separately with a mixed model (lme4: Bates et al., 2015; exactRLRT: Scheipl et al., 2008). These mixed models included period of test, shark size, trial number (for exploration) and nursery (when data sets included both nurseries) as fixed effect. Repeatability was tested

and calculated for both nurseries within the two age classes and for overall OS and YOY sharks and was calculated by dividing the random term (individual ID) by the total explained variance (individual ID + residuals). All analyses were performed in R (R Core Team, 2015).

RESULTS

One to three years old sharks

Behavioral syndrome

Sharkland

Sharks aged from 1 to 3 years from the Sharkland nursery showed a negative relationship between exploration and sociability; i.e. sharks that were more social were less explorative (Table 1). This negative relationship was not found in the other nursery (Table 1). Both behaviors were found to be correlated with body size (N = 49; exploration: p-value = 0.009; rho = 0.36; Social: p-value < 0.001, rho = -0.53). Controlling for body size decreased the strength of the correlation between the two behaviors but did not account for it (partial correlation; p-value = 0.0139, rho = -0.35). It should be noted that the observed correlation was mainly driven by tests in June 2012 where half of the SL OS sharks were tested for the first time (N=25, p-value=0.005, rho=-0.54).

While estimating covariance using mixed model, I found the confidence interval to slightly overlap with 0 (MCMCGLMM covariance estimate: N=69 individuals tested for both traits; -0.43 [-0.73; 0.039]) making interpretation more difficult. On the other hand, when size was removed from the model, exploration and social behavior were found to negatively co-vary (-0.61 [-0.79; -0.087]).

North sound

In contrast to SL sharks, in the NS nursery, the lack of covariance was apparent using both the correlation (Table 1) and the mixed model analyses (MCMCGLMM covariance estimate: N= 59; 0.10 [-0.25; 0.64]). However, when size was removed from the model, exploration and social behavior were found to positively co-vary (0.58 [0.13; 0.82]).

Table 1: Correlation estimates between exploration and sociability in the four categories of juvenile lemon sharks of interest in this study. YOY: young of the year, OS: from 1 to 3 years old, SL: Sharkland nursery and NS: North Sound nursery.

	NS	**SL**
YOY	N=68 p-value=0.68 rho=-0.05	N=49 p-value=0.21 rho=0.18
OS	N=21 p-value=0.18 rho=0.30	N=49 p-value=0.0005 rho=-0.47

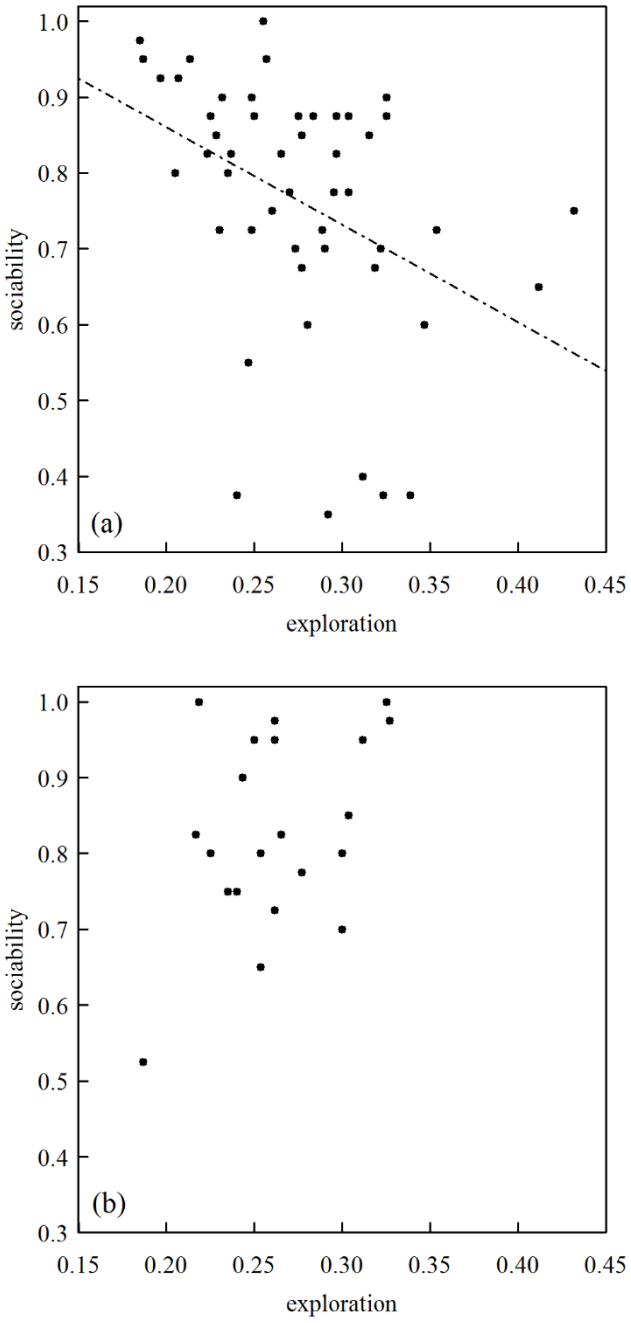

Figure 3: Correlation between exploration and social behavior is OS sharks from Sharkland (a) and North Sound nurseries (b).

Consistency

Overall OS sharks showed repeatability in both exploration and social tendency. Similarly, both traits were found to be repeatable for SL sharks. However only exploration was repeatable for NS sharks (see Table 2).

Table 2: Significance and estimation of repeatability of sociability and exploration in juvenile lemon. OS: from 1 to 3 years old, SL: Sharkland nursery and NS: North Sound nursery.

OS	SL	NS	ALL
Exploration	N_{ind}= 69 ind; $N_{ind\ rep}$= 26; $N_{obs\ ind\ rep}$= 60 p-value=0.0277 RLRT=3.8 Rep=0.44	N_{ind}= 59 ind; $N_{ind\ rep}$= 10; $N_{obs\ ind\ rep}$= 26 p-value=0.01 RLRT=4.88 Rep=0.46	N_{ind}= 128; ind; $N_{ind\ rep}$= 36; $N_{obs\ ind\ rep}$= 86 p-value=0.0036 RLRT=7.15 Rep=0.40
Sociability	N_{ind}= 69 ind; $N_{ind\ rep}$= 26; $N_{obs\ ind\ rep}$= 60 p-value=0.028 RLRT=3.64 Rep=0.335	N_{ind}= 59 ind; $N_{ind\ rep}$= 10; $N_{obs\ ind\ rep}$= 26 p-value=0.28 RLRT=0.30 Rep=0.10*	N_{ind}= 128; ind; $N_{ind\ rep}$= 36; $N_{obs\ ind\ rep}$= 86 p-value<0.001 RLRT=11.23 Rep=0.41

N_{ind}: Total number of individuals tested, $N_{ind\ rep}$: Number of individuals replicated, $N_{obs\ ind\ rep}$: Total number of replicated observations.

Young of the year sharks

Independent of where YOY sharks were caught, they showed no relationship between the two personality traits tested (Table 1). Further, no co-variance was found with a mixed model (data not shown). Similarly, YOY sharks did not show any repeatability in the two personality traits (Table 3). However, it should be noted that when size was removed from the model YOY sharks showed consistent individual differences close to significance in their exploration tendency (p-value=0.0536, RLRT=2.6, rep=0.29).

Table 3: Significance and estimation of repeatability of sociability and exploration in juvenile lemon.

	SL	NS	ALL
Exploration	N_{ind}= 50 ind; $N_{ind\ rep}$= 13; $N_{obs\ ind\ rep}$= 29 p-value=0.21 RLRT=0.67 Rep=0.35	N_{ind}= 78 ind; $N_{ind\ rep}$= 30; $N_{obs\ ind\ rep}$= 66 p-value=0.22 RLRT=0.54 Rep=0.18	N_{ind}= 128 ind; $N_{ind\ rep}$= 43; $N_{obs\ ind\ rep}$= 95 p-value=0.26 RLRT=0.36 Rep=0.12*
Sociability	N_{ind}= 50 ind; $N_{ind\ rep}$= 13; $N_{obs\ ind\ rep}$= 29 p-value=0.14 RLRT=1.26 Rep=0.25	N_{ind}= 78 ind; $N_{ind\ rep}$= 30; $N_{obs\ ind\ rep}$= 66 p-value=0.21 RLRT=0.59 Rep=0.20	N_{ind}= 128 ind; $N_{ind\ rep}$= 43; $N_{obs\ ind\ rep}$= 95 p-value=0.18 RLRT=0.75 Rep=0.13

YOY: young of the year, SL: Sharkland nursery and NS: North Sound nursery.

N_{ind}: Total number of individuals tested, $N_{ind\ rep}$: Number of individuals replicated, $N_{obs\ ind\ rep}$: Total number of replicated observations.

DISCUSSION

In this investigation, I examined the presence of a behavioral syndrome in a wild population of juvenile lemon sharks. Individuals were divided into their nurseries of capture (North Sound: NS and Sharkland: SL) and their age classes (young of the year and older sharks). I found a negative correlation between sociability and reaction to a novel-open field (mentioned thereafter as exploration) in non-new-born sharks (i.e. 1-3 years old) captured in SL. In the same age class, NS sharks showed contrasting results. Due to a potential lack of statistical power, it is yet not clear if they present a syndrome in the other direction (positive co-variance) or no syndrome. But it seems likely that sharks from these two nurseries differ. YOY sharks did not show any co-variance between exploration and social behavior for both nurseries. While examining repeatability, overall results indicated consistency for 1-3 years old sharks from both nurseries (except for sociability in NS sharks) and no consistency for

YOY sharks (but see discussion on exploration for YOY sharks). The smaller sample size for some of these categories (i.e. NS OS sharks and YOY sharks) makes interpretations difficult but the difference in syndromes along with varying patterns in consistency observed raises numerous questions for future investigations.

The key finding of this investigation is that sharks from the Sharkland nursey, from 1 to 3-year-old (SL OS sharks), showed a negative correlation between exploration and sociability tendency. In other words, the more explorative a shark is the less social it is. Nevertheless, one has to be careful while using phenotypic correlations (i.e. raw behavior correlations found here) as they do not prove the presence of a syndrome (Brommer, 2013; Dingemanse & Dochtermann, 2013; Garamszegi et al., 2015). This correlation could be created by within-individual co-variation (e.g., both axes correlated with the same uncontrolled environmental factor creating the observed correlation). However, I believe this to be unlikely because OS sharks from both NS and SL were tested during the same time periods using the same methodology. The fact that a difference in the syndrome was found between these two nurseries suggests biological rather than methodological causes. Using multivariate mixed modeling approach can be used to dissociate between within-individual and between-individual (i.e. syndrome) co-variation (Dingemanse & Dochtermann 2013). Unfortunately, I could not confidently prove that the correlation observed here is representative of a syndrome using mixed modeling (confidence interval estimating between-individual co-variance overlapped with 0). This confidence interval should, however, be taken with caution because of the small sample size available and the fact that juvenile lemon sharks have shown individual differences in habituation rate to open field which can decrease mixed model estimation of repeatability (**Chapter 2**). More data clearly need to be gathered before to conclude but these results strongly suggest the presence of a syndrome. Unfortunately, it difficult to discuss syndromes including sociability as little work has been conducted on

syndromes that include the sociability personality axis (Garamszegi et al., 2013). Nevertheless, despite limited data, the results from other species typically do indicate variation in this syndrome. For instance, our results agree with Budaev (1997) who found that less social European wrasses (*Symphodus ocellatus*) were more active in a novel open field. However, Cote et al. (2010) found a weak but positive correlation between sociability and novel open field in the mosquito fish. More generally, other studies have demonstrated a relationship between social behavior and social dynamic with other personality traits (e.g., Aplin et al., 2013; Croft et al., 2009; Kurvers et al., 2009; Pike et al. 2008). However, the use of various social proxies (e.g., leading, social network measures) and personality measures (e.g. boldness, novel object inspection) makes comparisons and any behavioral generalizations difficult. In addition, it has recently been shown that the correlation between novelty avoidance and aggression varies dramatically between years in the collared flycatcher (*Ficedula albicollis*; Garamszegi et al., 2015). This is problematic as most of our SL sharks of 1 to 3 years old where tested in June 2012. It therefore clear that my experiment needs to be replicated to look at changes between years and to increase sample size which will improve the use of mix modeling.

The strong variation present in the population of juvenile lemon shark studied dramatically reduces my sample size which prevents me to confidently interpret results for the other individual categories (i.e. NS sharks and YOY sharks). However, interesting questions are apparent which I believe deserve to be mentioned for future potential investigations. The data shows no syndrome or a positive syndrome present in non-new-born NS sharks which dramatically differ from SL sharks. This difference suggests some environmental components causing the behavioral syndrome studied here to vary. One potential candidate is predation risk differences. Indeed, there is evidence showing a higher presence of predator in SL than in NS (See for instance, Guttridge et al., 2012; Kessel et al., 2013). However, more

environmental data are necessary to be able to identify which environmental factors are responsible for the variation in BS. This represents a major challenge and likely demands the addition of supplementary populations of juvenile lemon sharks or other species with varying ecological contexts. However, these are the necessary steps to transfer knowledge from controlled environmental experiments to natural occurring conditions and provide a broader ecological context to animal personality. My results also suggest emergence of the syndrome and consistency during the first year of life of lemon sharks and not at birth. Indeed, I found no syndrome and no consistent individual differences in any of the nurseries in YOY sharks. One could argue that the lack of consistency is due to sample size and the fact that many sharks could only be tested twice instead of thrice (a few months after birth and only once when they are or passed 1 year old). Observing YOY sharks only twice was chosen to avoid inflating repeatability. Indeed, more than two tests would have led to multiple observations once they passed 1 year old (i.e. became consistent). Still, when combining both nurseries, dramatically increasing sample size, no consistency was found (as opposed to combined OS sharks) which strongly suggests a lack of consistency in this age category. At this stage, it is impossible to assess whether natural selection and/or individual development are responsible for the emergence of BS and consistency. Other studies have demonstrated that both mechanisms play a role into the development of personality axes and BS (e.g., Adriaenssens & Johnsson, 2013; Bell & Sih, 2007). Overall, as investigations accumulate, the environment in which individuals develop appears to play a big role in shaping personality (Edenbrow & Croft, 2011, 2013; Freund et al., 2013; Groothuis & Trillmich, 2011; Guenther, Finkemeier, & Trillmich, 2014; Rödel & Meyer, 2011; Urszán et al., 2015). In agreement, our study suggests that the BS is not present from birth making YOY sharks an interesting group to study in the future. Lack of long term consistency was also detected in OS NS sharks' sociability tendency as opposed to SL sharks in the same age class. The most parsimonious

explanation is the low sample size associated with this particular individual category and these results cannot be further discussed. Overall, these data indicate a strong variation in what is considered as one wild population of juvenile lemon sharks. Such variation, potentially due to environmental and ontogenetic differences, will likely occur in many other wild animals and should be taking into account by investigators. As illustrated here, a failure to do so might result in false rejection of a correlation between behaviors.

An interesting pattern was also apparent in YOY sharks' exploration. Repeatability in exploration was found to be on the boundary of significance when size was removed from the mixed model. This suggests that individual differences in size might create individual differences in exploration for YOY sharks. I would indicate some in born component to the exploration axis (e.g. heritability and or maternal effect) and fit with theories suggesting state differences between individuals as one of the potential causes for personality differences (e.g. Mcelreath & Strimling, 2006). Alternatively, the effect of size on individual differences could be due to the fact that larger individuals cross more areas in the open-field simply due to their size differences. This explanation would indicate a lack of personality during the first year (or first few months) of life of YOY sharks. Designing experiments that would distinguish between these two explanations would be worthwhile to understand development of personality in this species. One could allow sectors size to increase with animal size (using video recording) or develop other tests potentially less sensitive to size (e.g. emergence tests). In addition, it could be interesting to look into details of development changes of individuals through the first two years. While doing so habituation effects should be kept in mind (**chapter 2**).

Measuring personality in the field and especially in large animal such as sharks brings challenges (Finger et al., 2017 and introduction/discussion). I, however, argue that investigating wild populations and increasing species diversity is an important step to increase

our understanding of personality in an evolutionary and ecological context (Archard & Braithwaite, 2010; Dochtermann & Dingemanse, 2013; Réale et al., 2010). With this objective in mind, I demonstrated that a correlation between exploration and sociability could be found in juvenile lemon sharks. However, I detected marked variation in this BS and the presence of consistency in these two personality traits. This variation has led to many questions and research avenues that could contribute to a better understanding of animal personality emergence and maintenance.

5. General Discussion

A portion of this discussion is published (Finger et al., 2017)

5.1 DISCUSSION OUTLINE

Animal personality has been described in many taxa, from insects to primates (Bell et al., 2009; Gosling, 2001) including aquatic animals (Conrad et al., 2011). Despite all these studies, no data were available on elasmobranches personality at the beginning of this thesis. To fill this gap, I investigated different aspects of personality in the juvenile lemon shark. I demonstrated that sharks differ in their reaction to novelty. Then, I showed that they differ in their tendency to socialize when observed in captive social groups. Finally, I found a negative correlation between reaction to novelty and sociability in sharks from one nursery that are 1 year old or older. Even though the results are far from showing a complete picture, they are among the first steps in the study of personality in these animals. In addition, I believe that this work also contributed to and proposed methods to further improve our understanding (i.e. causes and consequences) of animal personality overall. Detailed discussions about each of these topics and their contributions to the field of animal personality can be found in their associated chapters (i.e. **chapter 2, 3 and 4**).

In this part, I discuss my results regarding two main topics which I believe to be important to the study of animal personality and sharks. First, I discuss the difficulty to interpret personality tests and, second, the ecological consequences of animal personality and its relation to species/ecosystem management. This allowed me to identify interesting research directions for the animal personality field and to illustrate the benefits of studying personality in sharks for the field itself and for the conservation of these animals.

Following these thoughts, the last part of this discussion focuses on demonstrating the achievability to investigate personality in large sharks. I begin with a brief mention of why

investigating sharks is important (These arguments plus others are repeated throughout the following text while being associated with illustrative studies/species). Then I mention some of the main experimental constraints and challenges of the study of sharks in captivity which make wild observations essential. I, then, show the feasibility to investigate consistent individual differences in sharks' natural behavior with a succinct review of wild studies. This overview lists studies from the literature that found variations between individuals. Most of these studies do not test or mention consistency in these differences and cannot be used as proof of personality. However, they highlight how widespread and potentially important these individual variations could be in sharks' everyday life and provide methods that will serve the development of shark personality research.

5.2 THE BABEL TOWER OF PERSONALITIES

One issue mentioned in this thesis is the difficulty to interpret personality tests. I further discuss this here as I believe this topic to be an important, but neglected, aspect of personality research that should be addressed (Toms et al., 2010, Réale et al, 2007; Burns, 2008; Carter et al, 2013; Beckman & Biro, 2013; Perals et al., 2017). Indeed, the lack of common terminology and methodology (see below for details) makes comparisons difficult between species or even between tests thought to represent the same personality axis.

Broadly speaking, personality has been approached in two different ways: the psychological (more human-oriented tradition) and the biological approach (more animal-oriented tradition). In the psychological approach, personality is organized in hierarchical structures under the mostly accepted Five-Factor Model (Koski, 2011b; Nettle & Penke, 2010; Toms et al., 2010). This approach usually uses behavioral rating based on questionnaires and has also been used in some non-human taxa (i.e. primates Uher & Asendorpf, 2008; Weiss et al., 2011; bottlenose dolphins, *Tursiops truncatus*: Highfill & Kucjaz, 2007). The biological approach (i.e. this thesis and most of animal personality literature) experimentally measures the reaction

of individuals subjected to different stimuli (e.g. novel environment: **chapter 2**, conspecific: **chapter 3**). The benefits of both approaches have been discussed at length (e.g. Uher & Asendorpf, 2008, Toms et al. 2010, Kosky, 2011a). However, one issue that I would like to stress is the difficulty to rate species taxonomically more distant from us. In this thesis for instance, one can easily understand that rating primates would be easier than rating sharks. In addition, the more hierarchical, multivariate description of the psychological approach can also make comparisons difficult with the more behavioral-units focus of the biological approach. Nevertheless, as the focus on behavioral syndromes increases (e.g. **chapter 4**), this gap could decrease. One could attempt to investigate syndromes that are representative of personality structures found in primates and humans and inversely. Overall, these differences could make comparisons difficult throughout the full animal kingdom until both approaches could be fully reunited.

Unfortunately, the difficulty of comparison between species also extends within approaches. Within the biological approach, discrepancies can arise due to biological and ecological differences between species. A shark cannot be tested in the same novel open field as a bird which led to different proxies used within the same type of experimental apparatus. For instance, Verbeek et al. (1994) tested great tits (*Parus major*) in a novel cage and measured time to visit trees in the experimental set up. Whereas in **chapter 2**, we measured reaction to novelty by recording activity in a novel open field. In the European wrasse**,** Budaev (1997) measured movements, freezing, hanging in midwater in a novel pen field whereas Watanabe et al. (2012) measured terrestrial hermit crabs' (*Coenobita clypeatus*) emergence time from their shells when placed in a novel open field. These differences in proxies used, in open-field test designs, in combination with species differences in perception of novelty (risky versus non-risky) might lead researchers to test different personality axes (i.e. boldness, exploration, activity) using this test. Therefore, despite the widespread usage of novel open field tests

(vertebrates: Boon et al., 2007; Budaev, 1997; Burns, 2008; Dingemanse et al., 2012; Rodríguez-Prieto et al., 2010; Verbeek et al., 1994; invertebrates: Tremmel & Müller, 2012; Watanabe et al., 2012), it might be premature to consider them as testing the same personality axis and therefore as having similar proximate/ultimate causes or similar ecological consequences. Nevertheless, the successful use and widespread applicability of this test makes it an interesting candidate for across species comparison which makes it all the more interesting to further investigate.

Similar difficulties could be noted for proxies used to measure sociability in the field of animal personality. In **chapter 3**, social occurrences were only validated when the focal individual actively interacted, whereas being followed by another individual (without following) was not considered as social. If carefully considered, one can see that this measure is less sensitive to group composition. Indeed, the tendency of being followed is likely dependent on the proportion of followers in the group (at least in our system; see **chapter 3** for more details) and, therefore, this measure was meant to measure the individual tendency/willingness to socialize. However, many other proxies and methods have been used to test sociability personality. The diversity of methods can be illustrated with just a few examples from the literature. For instance, Cote et al. (2010) used a binary choice to test personality in the western mosquitofish. A similar method was used to test sociability in the spider *Anelosimus studiosus* (Pruitt et al., 2011). As in chapter 3, other studies have tested individuals in groups. For instance, Krause et al. (2017) used social network analyses in the guppy. Social network analysis is a powerful tool (Wilson et al., 2013) but adds numerous available proxies further complicating cross studies comparisons. Or while tested in groups, leadership has also received some attention (e.g. Ward et al., 2004, Burns et al., 2012, Kurvers et al., 2009). The usage of more descriptive and detailed behaviors such as grooming, submission, and play have been used in multivariate analyses (e.g. Koski, 2011a; Weiss et al.,

2006) in primates. This latter approach has often led to different social behaviors being associated with different personality axes (e.g. Weiss et al, 2006). In my opinion, this diversity illustrates the need for converging methods to measure social personality but also reflects that two personality axes (i.e. sociability and aggressiveness: Réale et al., 2007) might not be enough to fully apprehend the complexity and diversity of social dynamics in the animal kingdom. In future, it is important to identify whether and which axes can be extracted if one wants to fully understand the impact of personality on social dynamics.

As mentioned above, the diversity in measures used for most of personality tests are created, to some extent, by the animal diversity. It is then clear that such variation cannot be avoided. However, what can be done is working toward a more unified field by developing studies that improve result interpretations. For instance, in **chapter 2**, I proposed a test that allowed me to show how activity in a novel open field was (at least in part) a measure of reaction to novelty and not activity. However, the next step will be to use validity tests to understand if we are testing boldness or exploration (Beckmann & Biro, 2013; Burns, 2008; Carter et al., 2013; Perals et al., 2017; Toms et al., 2010; Uher & Asendorpf, 2008). Similar frameworks should be developed to investigate consistent individual differences in sociability and the independence of the different proxies used. In addition, multivariate analyses could prove very useful to identify separate personality axes when enough data can be gathered. However, while performing validity tests or multivariate analyses in animals, it is important to consider the presence of syndromes between axes. Two positively correlated behavioral measures might not represent the same personality axis but a syndrome which could be absent in another population of the same species. It will therefore be important to identify when and where syndromes are present or absent by comparing populations or subpopulations (e.g. **chapter 4**). As the number of species shown to have personality increases, it is becoming

critical to provide confident information on what is being tested and if they share similar ecological consequences in the wild.

5.3 PERSONALITY, ECOLOGY AND CONSERVATION

In recent years, the relation between personality and sensitivity to human harvesting has gained a lot of interest (Arlinghaus et al., 2017) and it has been argued that personality should be included into population management plans (Conrad et al., 2011, Mittelbach et al., 2014). Indeed, it is known that behavioral differences can impact likeliness of catchability (e.g. Biro & Post 2008; Uusi-hakken et al., 2008) and that these differences in catchability can lead to selection against personality related life history traits (e.g. parental care: Sutter et al. 2012, growth rate: Biro & Sampson; 2015). Unfortunately, no research investigating a potential link between personality in sharks and human harvesting is available. I believe this to be a critical gap within our knowledge that could prove to be detrimental to marine ecosystems. Indeed, a large proportion of shark species present slow growth and reproduction rates, and long-life spans. Their diversity and important functional roles in the top-down control of marine ecosystem structure and function (Ferretti et al., 2010; Heithaus & Dill, 2002) make these animals very important in the marine landscape. Therefore, scientists have raised concerns over the impact of over exploitation on these animals and the indirect effect that their declines could have on entire ecosystems (Dulvy et al., 2014; Heithaus et al., 2008; Stevens et al., 2000; Worm et al., 2013,). One can easily conceive that miscalculated management plans could have non-negligible impacts on the conservation of sharks (and other mega fauna sharing similar biological characteristics). Therefore, a research line aiming at understanding the relationship between personality and conservation would be interesting and necessary. However, such an understanding will only be reached after the ecological consequences of personality are fully grasped. I will describe some of these potential future avenues for sharks that have been and are still developing in other taxa. While doing so I use my results in the

light of the animal personality literature to argue that consistent individual differences in sharks have likely strong consequences for their ecology and conservation.

One important step to understand ecological consequences of personality is to demonstrate long-term consistent individual differences in wild animals. Such studies are rare in the field of animal personality (Archard & Braithwaite, 2011) but some have demonstrated long term consistent individual differences in wild population (e.g. Aplin et al. 2015; Cote & Clobert 2007) and this thesis has the only evidences of long term consistency in wild sharks (**chapters 3 and 4)**. This is an important research line to demonstrate and understand the ecology of individual differences. The fact that long term consistency is found in a diverse array of taxa (e.g. reptiles, birds, sharks) indicate that indeed personality has a strong impact on animal every-day life throughout the animal kingdom and is likely to be found throughout the animal kingdoms (including other shark species).

Then it will be important to understand the relation between fitness parameters and personality axes. This relation has been demonstrated in some species (Biro & Stamps, 2008; Smith & Blumstein, 2008) indicating that an impact of personality on fitness traits should be expected in most cases. Therefore, it is important to continue this research and extend it to the personality axes and species of focus. For instance, these data do not exist for sharks even though current knowledge suggest a potential relation between fitness and individual differences. Juvenile lemon sharks (age-1) with higher growth rates and larger sizes than their conspecific have been shown to have a lower survival (Dibattista et al. 2007). In addition, it has been demonstrated that fast growing individuals fed over more exposed (i.e. riskier) areas than slower growing individuals. (Hussey et al., 2017). I found this particularly interesting when related to the recent finding that life history traits were correlated with individual differences in movements and prey selection in the wild perch (Nakayama et al., 2017). Taken

together these studies strongly suggest that, like in bony fishes, the relation between personality and life history traits could be present and should be investigated in sharks.

Another interesting avenue would be to investigate the ontogenetic development of personality (Groothuis & Trillmich, 2011; Stamps & Groothuis, 2010). This could be used to inform the distribution of individual personality types expected to be found in the following generations of harvested fish populations. For instance, the distribution might be different if personality was found to be solely heritable or to be solely dictated by the environment. Results from **chapter 4** indicate that development might have an important part for the juvenile lemon sharks as shown in other studies (Edenbrow & Croft, 2011, 2013; Freund et al., 2013; Groothuis & Trillmich, 2011; Guenther et al., 2014; Rödel & Meyer, 2011; Urszán et al., 2015). However, it is known that natural selection also plays a part into emergence of personality (Adriaenssens & Johnsson, 2013; Bell & Sih, 2007). In addition, it has been demonstrated that some axes are heritable (e.g. Van Oears 2004) but that the extent of heritability could also vary between populations and environmental conditions (Dingemanse et al., 2009). It is still unclear which personality axes are more plastic and in which conditions. Interestingly, predation has been shown to have an impact on the genetic expression of individual differences (Dingemase et al., 2009) which, again, illustrate the necessity to consider high trophic position animals as potentially different from the usually investigated animals. Overall, more work in this direction is needed if one wants to understand evolution of personality or impact of fishing on population.

As described here, there are many interesting results showing the importance to consider personality within population/ecosystem managements. However, if only, typical, practical to study and publication productive species are studied, one can wonder how useful such management recommendations could be if they cannot be applied to key-stone, high

trophic position animals such as sharks. I believe that this thesis is a good stepping stone to do so and I hope that it could help toward the development of more shark personality studies.

5.4 PERSONALITY AND INTER INDIVIDUAL VARIATION IN THE WILD

Along with the need to better understand individual differences in sharks for conservation purposes, most of sharks' life history strategies, their phylogenetic positions (i.e. basal to all vertebrates tested for personality) and trophic positions make them an interesting taxon to study relative to most aquatic animals commonly investigated in animal personality. For instance, as stated in **chapter 3**, the lack of predation risk for some shark species might lead to different mechanisms for schooling behavior (Klimley, 1985) than for smaller organisms usually studied (Krause & Ruxton, 2002). This in turn could lead to different ecological consequences compared to other species. Similarly, animals that don't have a high predation risk throughout most of their life span might perceive a novel environment differently (see **chapter 2**) and have different costs of exploring. On the other hand, personality might be dictated during their juvenile stage when predation risk is higher (see **chapter 4**) to be then maintained throughout their life span. If this is the case, then similar mechanisms responsible for the emergence and maintenance of individual differences might be shared between sharks and smaller, high turnover generation organisms. Finally, some shark species remain relatively small and sensible to predation giving the opportunity to compare between phylogenetically closely related species with different ecology. Overall studying sharks might lead to a different perception of the causes and consequences of personality and contribute to a better management of marine systems. However, all studies on shark personality have been conducted on juvenile or small shark species (see introduction). There is a need to test larger sharks to grasp the diversity of these animals. Unfortunately, it is difficult or impossible to keep large aquatic animals in captivity and their range of behavior is dramatically reduced. For instance, large-bodied marine animals, including many sharks and

close to half of chondrichtyes species, undertake migrations as part of their life cycle (Grubbs et al., 2010), and require considerable space to demonstrate natural prey–capture behavior (e.g., breaching behavior in great white sharks, *Carcharodon carcharias*: Martin et al., 2005; patch foraging in basking sharks, *Cetorhinus maximus*; Sims et al., 2003), or reside in depths exceeding 200 m (Cotton & Grubbs, 2015). As such, experiments of captive sharks are difficult, if not impossible to implement which could prevent personality testing in many species. Therefore, a large part of this research would need to go in the field, which seems difficult at best. Nevertheless, I believe that studying large sharks in the wild is realizable and to argue this point I will finish this thesis with reviewing studies demonstrating consistent variation in wild sharks and discuss others that have described individual variation. Overall, I hope these studies could be used as stepping-stones to develop research on sharks and other large marine animals.

5.4.1 Evidence for personality in the field

As already described in **chapter 1**, evidence for personality in the wild was demonstrated in the Port Jackson sharks (Byrnes et al., 2016b). I would like to repeat that this study is applicable to numerous species, including bottom dwelling sharks, such as nurse sharks or catsharks providing an interesting guideline for future studies. However, it remains unclear how this could be adapted to larger animals or relate to naturally occurring behaviors. It will be also important to develop less intrusive methods.

5.4.1.a The juvenile bull shark as a model species for personality research

Investigations of juvenile bull sharks (*Carcharhinus leucas*) were successfully used to detect consistent individual differences in behavior (Matich & Heithaus, 2015), revealing their study system as particularly promising for the study of personality in sharks. Prior to discussing this study, it is interesting to note parallels with the juvenile lemon shark studies described above.

Like lemon sharks, which use mangrove fringed habitats as nursery areas, juvenile bull sharks can also be found using estuarine or freshwater habitats. Some of these habitats are known to be safer (less predation) but less productive (less food) further upstream (further away from the marine environment) (Matich & Heithaus, 2015), and so are comparable to what is experienced by juvenile lemon sharks in Bimini. These similarities suggest that juvenile bull sharks face similar trade-offs between benefits and risks, which could promote individual differences. Indeed, Matich et al. (2011) found that individual juvenile bull sharks from their study site differed in their diet. Some individuals fed in the riskier marine food web and others in the safer estuarine habitat, which led the authors to propose that individuals differed in their risk-benefit strategies. More recently, in the same system, juvenile bull sharks were found to differ in their movements and in the portion of the estuary they used, with some being detected more often in riskier locations (e.g., downstream near the mouth) than others (Matich & Heithaus, 2015). These consistent individual differences were documented for at least four months and were independent of age class. Unfortunately, these investigations were performed on different groups of individuals leaving the existence of a potential relationship between individual differences in estuary use and feeding habit unproven.

It is important to note that estuarine systems can be heterogeneous and so, until there is evidence for personality in a more controlled environment, it is challenging to disentangle what could be related to responses to environmental conditions or to individual behavioral differences. For instance, Ortega et al., (2009) investigated movement in juvenile bull sharks in Florida and in another river system. Similarly, they found differences in movement between two groups of juvenile bull sharks but explained that these could have been related to the locations within the river and the differences in habitat within these areas. Regardless, juvenile bull sharks are a promising model with which to investigate consistent individual differences in behavior. The heterogeneity of predator pressure and resource abundance in the

juvenile bull sharks' nursery habitat contributes to the likelihood that personality differences are present in this species. Longer term studies along with a demonstration of a long-lasting relationship between movement differences and feeding location differences (risky marine web food versus safer estuary) or life history traits (e.g., growth rate and survival) would strongly suggest that these differences reflect (at least partly) consistent individual differences and demonstrate the ecological importance of such differences. In the best scenario, individual differences should be investigated in controlled captive or semi-captive conditions and then in the field (e.g., Herborn et al., 2010; Yuen et al., 2016). This strategy would, for instance, allow researchers to further investigate if habitat use variability is due to differences in boldness, dominance, sociability, or exploration.

5.4.1.b Behavioral assays in large free ranging sharks

Being usually shy, wide ranging and aquatic animals, sharks behavior is difficult to observe in many species. The need to score the same individuals multiple times, to demonstrate personality, logically further amplifies this difficulty. However, as shark personality receives more attention, systems and methods are likely to be identified and developed.

For instance, white sharks provide a potential model to study personality in a large, upper-trophic predator. White sharks can be attracted to research boats using bait and repeatedly observed over months or years, as demonstrated by the development of eco-tourism in South Africa (e.g., Laroche et al., 2007). This opens up the possibility to observe the same individual multiple times. Furthermore, these sharks have been observed inspecting novel objects on the water surface (Hammerschlag et al., 2012). These characteristics were taken advantage of by William Hughes, Marlene Stürup and colleagues in their investigation of individual differences in the behavior of white sharks, and the preliminary results are encouraging (William Hughes, personal communication). If these tests are applicable to personality research, they might provide a method for testing personality in large sharks in the

wild. These methods could be used to further investigate the relationships between personality traits (such as novel object inspection) and individual differences in observed behaviors, such as movements, space use, hunting strategy, social interactions, feeding habits, and more, to be described below.

The examples given above in addition to lemon sharks and catsharks (see introduction) provide a solid ground for future investigations aiming at investigating the transferability of personality into the wild and consistent individual differences in natural behavior. Indeed, combined together they provide different methods to test personality in captivity and in the wild. Therefore, crossing methodologies will provide a strong step forward into the study of personality in wild sharks. Considering the growing evidence for inter-individual variability in their natural behavior across several species with diverse taxonomy, biology, and behavior, such effort is of critical importance. In order to argue this point, the following paragraphs will discuss such studies.

5.4.2 Evidence for inter-individual variation in shark behavior: reasons to study shark personality

In the following part of this chapter, I describe the growing evidence for inter-individual variability in the natural behavior of elasmobranchs across several species with diverse taxonomy, biology, and behavior. These anecdotal descriptions of variation between individuals do not constitute proof of personality, and I do not intend to use these descriptions as such. Indeed, little attention has been paid to testing if individual differences in behavior are consistent (a key concept to personality) and if these differences have fitness consequences (e.g., growth rate, survival, reproduction) in the field. Despite the dearth of studies that test for consistency, I want to illustrate how, if proven to be related to personality, further investigating the variability between individuals could improve management success and our understanding of animal personality. Because such studies could inspire further work

on shark personality, I describe which tools and methods were used in these studies. In this section I selected a few studies to illustrate and discuss differences in movements (e.g., localized and large-scale) with a brief discussion about incorporating personality variables in the design of marine protected areas. In addition, I describe the rationale for studying personality in large, low predation-risk predators, and the potential for strong impacts of individual differences on ecosystems and sensitivity to wildlife tourism. Finally, I discuss preliminary evidence for differences in the social behavior of sharks and emphasize the importance of investigating personality in other elasmobranchs.

Understanding elasmobranch movement is considered as a critical step to improve their conservation (Chapman et al., 2015; Papastamatiou & Lowe, 2012). Data generated from these studies are crucial for delineating key areas that require protection, for example sites of parturition or aggregation (e.g., Mucientes et al., 2009). Such engagement has led to an explosion of studies on shark movements, development of technologies, and modern data analytic methods (see review: Hussey et al., 2015; Jacoby & Freeman, 2016). This effort has unraveled inter-individual differences in aspects of localized and large-scale movements.

The use of core areas has been documented in numerous shark species. These demonstrations have provided a large amount of data on movements in sharks and have revealed individual differences in uses of these areas. In addition to being important to animal ecology and survival, the fact that some sharks use core areas represents an interesting methodological advantage. Indeed, sharks' regular use of the same area for long periods of time allows researchers to follow individuals for extended periods (e.g., 3.5 years: Papastamatiou et al., 2010) and to then perform finer scale investigations. Understanding individual differences in movements around and in core areas can contribute to the development of accurate and efficient protected areas (i.e., marine protected areas, no-take zones). For instance, while focusing on protecting only those core areas, sedentary individuals

will be artificially selected for (Kaplan et al., 2014). If such differences are shown to be consistent and related to life history traits, this artificial selection could have a strong impact on the conservation of the species. Illustrating this point, many studies have found evidence for and/or discussed individual differences: adult blacktip reef shark, *Carcharhinus melanopterus* (Papastamatiou et al., 2010), scalloped hammerhead (Ketchum et al., 2014; Klimley & Nelson, 1984) and grey reef shark, *Carcharhinus amblyrynchos* (Field et al., 2010; McKibben & Nelson, 1986). Interestingly, some of these examples mention differences in other behaviors (e.g., social and agonistic behavior) revealing these systems as potentially good sources of data for future studies on personality.

Similarly, individual differences could be observed in large-scale movements (e.g., across international boundaries or oceans). Individual differences in such movements were, for instance, documented for blue sharks, *Prionace glauca* (Vandeperre et al., 2014), which were migrating throughout a large part of the North Atlantic in summer months. In Australia, bull sharks (Espinoza et al. 2016; Heupel et al., 2015) showed marked individual differences in their migration patterns. Examples of variation in destination, timing, and/or the extent of migration were also documented in spiny dogfish, *Squalus acanthias*, (McFarlane & King, 2003) throughout the Pacific, bull sharks in Australia (Espinoza et al., 2016), and in tiger sharks (*Galeocerdo cuvier*: Meyer et al., 2010; Papastamatiou et al., 2013). In addition, a promising phenomenon describing individual variation is partial migration (i.e., when only a portion of the population migrates). Little work has been performed in sharks, but partial migration is expected to have strong ecological and evolutionary impacts and important implications for fisheries management (Chapman et al., 2012; Chapman et al., 2015). Interestingly, differences in migration have been related to personality in fish (Chapman et al., 2011). No such association was investigated in sharks; however, in Hawaii, where some tiger sharks were resident and others were transient, returning for short foraging excursions (Meyer

et al., 2010), one proposed explanation for the variation was individual differences in cognitive maps due to initial differences in exploration. If this is the case, then it would strongly support personality as one cause for differences in large-scale movements in tiger sharks. And, if proven to be true and some individuals consistently migrated whereas others did not, then their conservation status might differ (e.g., differing legislation across borders) leading to selection favoring certain personality types.

As mentioned throughout this thesis, investigating personality and its effect on the behavior of large upper-trophic predators, such as tiger sharks or great white sharks, is critical for a more complete understanding of individual difference effects on these species' ecology but also throughout their ecosystems. Indeed, these large, predatory animals have a strong impact on their ecosystems. For instance, they play a role in coupling otherwise discreet food webs (Heupel et al., 2015; Matich et al., 2011; Rooney et al., 2006) and can impact prey behaviors. Such effects can be expected to occur throughout the food web where these sharks are present because they are known to target and, therefore, influence the behaviors and habitat use of other top predators, including marine mammals, such as bottlenose dolphins, *Trusiops aduncus* (Heithaus & Dill, 2002) or Cape fur seals, *Arctocephalus pusillus* (Towner et al., 2016). If individual differences in movements or feeding habits are consistent, then these differences could have large ecological ramifications throughout the migratory range of these large predators. Accordingly, individual differences were observed in tiger shark movements (Afonso & Hazin, 2015; Heithaus et al., 2002; Meyer et al., 2010; Vaudo et al., 2014) and in great white shark hunting strategies (Towner et al., 2016). The differences in hunting strategy were consistent over short time periods (over a month: Towner et al., 2016). As explained by the authors, a long-term investigation would be useful to provide evidence for individual specialization and an understanding of the impact that these findings have on prey behavior and foraging success (Towner et al., 2016).

Along with individual differences in behavior, great white sharks vary in their dietary shift with age and in their diet specialization. Researchers classified individuals as either specialists, generalists, or intermediary (Kim et al., 2012). Unfortunately, these studies were conducted in different locations; therefore, I can only speculate whether such differences in feeding habits are related to individual differences in behaviors of great whites as observed in other taxa (Toscano et al., 2016).

Despite the focus on the most well-known species, other large sharks that have received less attention are as important and have similar impacts on their ecosystems. For instance, the broadnose sevengill shark, *Notorynchos cepedianus*, is known to prey on other elasmobranchs and marine mammals (Abrantes & Barnett, 2011). Marked individual differences in movement and habitat use were found in this species. In addition, preliminary evidence suggested that there were diet differences between individuals at the study site. However, the authors explained that, due to unknown winter residency locations for the sharks, it was difficult to draw strong conclusions on this later point. In view of these few studies, it seems important to verify how common individual differences are in large sharks and how these differences impact ecosystems. These observations, combined with the possible existence of individual differences in large-scale movements leading to a complex network of linked ecosystems, suggest that underestimating individual differences could hinder our ability to understand and protect marine ecosystems.

Large charismatic sharks such as the tiger or great white shark have become stars of provisioning wildlife tourism and the potential effect of this activity has raised concerns (Gallagher et al., 2015). Again, it is worth bearing in mind that these effects may not hold for all individuals in the population. Indeed, the impact of shark cage-diving operations on great white sharks' movements varies between individuals (Huveneers et al., 2013). Such differences, if consistent, could be an example of individual differences in attraction to

novelty or in reaction to what might be considered as a potentially dangerous stimulus (dimensions of personality termed neophilia and boldness, respectively; Réale et al., 2007). If a link between personality and individual differences in reaction to ecotourism is demonstrated, behavioral observations with the participation of commercial boats could lead to the creation of a personality database.

Studying a variety of organisms with different life history traits and ecological conditions is needed to understand the predictors of animal personality (Réale et al., 2010, 2007). Therefore, testing and investigating personality in large upper-trophic predator sharks could also be rewarding for the field of animal personality. Indeed, large predators have a very low predation risk compared to most species that are investigated in animal personality research. Therefore, exploring personality in these species would add important data to the discussion on predation as one of the potential mechanisms for emergence and maintenance of animal personality. Similarly, the diversity of elasmobranchs does not stop at sharks. In fact, along with skates, rays, and chimaeras, sharks represent their own evolutionary lineage, and, as mentioned before, are highly diverse in their behavior and ecology. This is therefore an opportunity to add important comparative data. Unfortunately, less work has been conducted on other elasmobranchs. Still, such variation has been documented in a handful of ray species. For instance, individual differences in activity and residence time were found in the cownose ray, *Rhinoptera bonasus* (Collins et al., 2007) and in the movement pattern of manta rays, *Manta alfredi* (Papastamatiou et al., 2012). Notably, adult cownose rays and other rays have successfully been held in captivity for extended periods of time (Fisher et al., 2011), and so provide an opportunity to link behavioral traits observed in captivity to those observed in the wild. To my knowledge, no personality research has been conducted on captive rays or skates, but I hope to see research move in this direction.

Along with increasing the diversity of species, the behavioral complexity of elasmobranchs provides an opportunity to increase the range of behaviors screened for individual differences. This is the case for social behavior in sharks, which has attracted a lot of attention (Jacoby et al., 2012), including recent findings on individual differences in sociability (see Jacoby et al., 2014). Understanding more about the dynamics of shark social behavior is important as concentrations of sharks can easily be targeted by spatially focused fishing (Jacoby et al., 2012; Mucientes et al., 2009). Considering that some personality traits (e.g., activity and boldness) can lead to disproportionate capture rates (Biro & Post, 2008), understanding the presence and extent of social differences seems necessary to improve fishery and ecosystem management. Furthermore, many questions concerning social dynamics in animals and the role of personality differences in groups remain (Farine et al., 2015; Wolf & Krause, 2014, **chapter 3**). Adding taxonomic diversity will contribute to a more global understanding of personality role in social group structures.

In the wild, juvenile lemon sharks differ in their tendency to lead groups (Guttridge et al., 2011). Differences were found to be size-dependent with larger individuals leading groups more frequently. However, there were instances where smaller individuals were observed to lead groups (T. Guttridge, personal communication). Future work should investigate how much these differences relate to personality and not confounding factors, such as age and size. Further individual differences were observed in the social behavior of blacktip reef sharks. Researchers measured gregariousness as the size of the group in which the individuals were observed (Mourier et al., 2012). They found that individuals differed consistently in their preferred group size. In addition, this investigation revealed the presence of distinct communities with varying social dynamics. More personality-focused investigations controlling for confounding factors (e.g. size, sex, and social environment) using the same method could give valuable information on shark personality in the wild. Over the long term,

this method and system could provide a good opportunity to study the relationship between personality and social dynamics in large marine vertebrates. Furthermore, this could be extended to additional elasmobranch species that form predictable aggregations, for example, whitetip reef sharks, *Triaenodon obsesus* (Whitney et al., 2012), whale sharks, *Rhincodon typus*, and manta rays (Rohner et al., 2013).

Another aspect of shark social dynamics worth exploring is the observation of differences in social ranking (e.g., dominance, agonistic behavior). Such differences have been shown to be consistent in bony fishes (McGhee & Travis, 2010) and related to other personality traits, including boldness and aggressiveness (Colléter & Brown, 2011) and reaction to stress and aggressiveness (Øverli et al., 2004). Interestingly, agonistic behaviors (e.g., head shakes or corkscrew swimming) were displayed by scalloped hammerhead sharks (Klimley, 1985). These sharks performed such behaviors to retain or obtain a central position within the large school they form. Unfortunately, whether these individuals consistently performed such behaviors and were more successful at occupying central position was not tested. The author interpreted the central position within the school as providing a social advantage to individuals, but not as a means by which individuals can avoid predators. This interpretation for occupying a particular position contrasts with the interpretation of this behavior for most schooling aquatic organisms. Indeed, in fish schools that are subject to high predation, positions are associated with varying degrees of risk (e.g., being at the front of the school is riskier than being inside the school; Ward et al., 2004). Because of this differing schooling function in the scalloped hammerhead shark, it would be interesting to determine whether individual differences in this behavior exist and how these differences are maintained in this species (or other with similar characteristics).

5.4.3 Tools for studying shark personality in the wild

In this part of the discussion, I highlighted studies that provide evidence for individual differences in wild shark behavior along with the tools and methods used to study personality in these populations (Table 1). Following this, I now emphasize the availability of former methods or data that, if revisited, could be used to investigate elasmobranch personality in the wild. I then briefly mention other tools that have been used in ecological and behavioral studies on sharks that will likely enhance the study of personality in these animals.

One behavior that could provide interesting data is the reaction of sharks to divers or other intrusive stimuli. Martin (2007) reviewed agonistic postures of sharks and how scuba divers triggered such reactions. Individual differences in agonistic response to divers has, for instance, been mentioned in grey reef sharks (McKibben & Nelson, 1986) suggesting a promising use of this approach. Using these observations as a starting point, remote-controlled craft equipped with cameras could be used to investigate personality traits such as boldness or neophilia, safely, in numerous species.

Existing data can also be used to test questions regarding animal personality. So far, no studies have taken this approach to investigate personality but present examples of re-analyzed data revealed inter-individual differences in movement behavior. For example, Papastamatiou et al. (2011) re-analyzed acoustic tracking data collected from tiger sharks, common thresher sharks, *Alopias vulpinus*, and blacktip reef sharks, and found individual differences in the movement patterns of tiger and thresher sharks. This illustrates the potential of the large amount of available data on elasmobranch movements. Once investigated under the animal personality framework, these data could become a useful source of information.

Table 1: Common methods used to investigate natural behavior of large aquatic animals.

Method	Technique
Acoustic telemetry	Acoustic tags fitted to animals autonomously transmit positioning data to static receiving stations (passive tracking) that can be retrieved periodically or to mobile "real-time" receiving stations (active tracking) for example on a pursuit vessel.
Satellite telemetry	PSAT (Pop-up Archival Satellite Tags) gather data on a variety of measurements (i.e. temperature, pressure, luminosity) while attached to the animal. Observations are sent to land based receivers via orbiting satellites once tags are detached from the animal. SPOT (Smart Position and Temperature tags) data on a variety of measurements (i.e. temperature, pressure, luminosity). Observation are sent to land based receivers via orbiting satellites each time the antenna is out of the water (i.e. when the sharks' fin is out of the water for tags fitted to dorsal fins).
Crittercam	Crittercams are small animal-borne video cameras that record the behavior of its bearer. They are mostly used for predator-prey encounter studies.
Photo-Identification	This technique consists of identifying unique features on an animal that are consistent through time. Pictures from recreational divers or the scientific team can be compared to previous images and individuals can be identified and observed through time. In Elasmobranchs, fin edges, ventral patterns, scarring or skin patterns have been successfully used to identify individuals, multiple years in a row.
Tri-axial accelerometer	Tri-axial accelerometer data loggers have revolutionized studies of animal behavior and are providing unprecedented new insight into the biomechanics of shark swimming. These devices measure accelerations due to gravity in 3-dimensions, and can be used to reconstruct a high-resolution record of shark body movements, including tail beat frequency and amplitude.
External tagging	Another technique used for individual recognition is through external tagging. Each individual can receive a tag that can be easily recognized (specific tag number, color, shape). This can allow the participation of recreational divers into the studies if necessary.

In their investigation, Wilson et al. (2015) measured individual swimming activity using accelerometers (see Table 1 and reviews by Shepard et al., 2008 and Wilson et al., 2006). Accelerometers have been successfully used on sharks (Bullock et al., 2015; Gleiss et

al., 2013; Whitney et al., 2007). These devices generate large data sets for researchers (i.e., continuous recording of tri-axial acceleration to quantify, for instance, locomotor activity and deduce body motion and posture), and these data could be used to test for and investigate individual differences.

Recently, new tools have been developed to investigate social behavior in such a way that direct observations are not required. Guttridge et al. (2010) made use of 'proximity receivers', small ultrasonic acoustic receivers that can be placed on focal animals to record signals sent by acoustic tags deployed on other individuals. These devices can be set to receive signals at close (e.g., < 10 m) or far distances (e.g., 100 m), allowing researchers to record the proximity of interactions. This technology could generate high resolution data and enable researchers to study social interactions in sharks over long periods of time (see also Haulsee et al., 2016). In the same vein, the development of acoustic technology (Hussey et al., 2015) has seen the parallel development of co-occurrence analysis (Jacoby & Freeman, 2016). Co-occurrences between individuals (detection of two or more individuals at different locations in a certain time interval) can be obtained using acoustic passive tools (see Table 1) and then used as a proxy for social interactions between individuals (Krause et al., 2013). Furthermore, fine scale positioning using acoustic technology permits researchers to almost continuously and simultaneously record the position of different individuals allowing researchers to investigate social behavior and aggregation of sharks. This method has been used to study the social dynamics of spotted wobbegong sharks, *Orectolobus maculatus* (Armansin et al., 2016), but consistent individual differences have not yet been examined.

To study the ecology of leopard sharks (*Triakis semifasciata*) at the population level, Nosal et al. (2012) used aerial balloons. One could also conceivably use drones to follow particular individuals and observe behaviors of interest. Drones and balloons are useful technologies that allow researchers to observe cryptic animals such as sharks without

disturbing these animals (Kiszka et al., 2016). Such methods can be applied only to particular environments, namely those in which one can maintain sight on the focal individual. Furthermore, these technologies have to be used in combination with methods for confirming the identity of the focals (e.g., former localization using acoustic tags). When these conditions are met, drones and other new technologies could become powerful tools for gathering detailed natural behavior about individuals.

5.4.4 Summary

I illustrated how studying personality in sharks could contribute to a better understanding of animal personality evolution and of the ecology of sharks and their ecosystems. Unfortunately, most of the examples do not consider personality as a potential explanation and, therefore, neglect to test if individual differences are consistent. This is unfortunate because, if some of the differences described in this section are consistent, they could have strong ecological implications. I mentioned, for instance, how variation in localized movements around home ranges or refuges, in large-scale movements, in social behavior, and in intra-population differences in feeding habits are potentially related to these behavioral differences. Because these differences can impact elasmobranch conservation or conservation of the ecosystem on a large-scale, it is important to consider personality within sharks' and other elasmobranchs' biology. Interestingly, such individual variation was also found in large apex predators under low predation risk. As mentioned before, this is of interest because predation risk is a central cause within the animal personality literature and determining whether such large predators exhibit personality could provide insights into the mechanisms that maintain animal personality variation.

5.5 CONCLUSIONS

Research on personality in sharks is in its infancy. Consequently, this thesis was strongly focused on developing methods to investigate personality in a wild population of sharks. I believe to have clearly demonstrated that personality can be found in wild sharks. This is an important step forward as this is a push toward testing animals that differs from the short generational times species usually tested in this field. In addition, I believe that my results and general discussion also demonstrate that contemporary animal personality questions can also be investigated in sharks. Still, my results are only a first glimpse and much more remains to do in the future, but, as the importance of individual differences is being appreciated more by researchers, I believe that new methods, systems and models for studying personality in sharks will developed. Accordingly, in this thesis, I have, also argued about the interest, necessity and feasibility of investigating large sharks in the wild. Overall, I hope that this thesis will contributed to the increase in studies on shark personality. Their body size and underestimated shyness, makes studying their personality a challenge that is not encountered in most model species used for personality research. However, as demonstrated and discussed in this thesis, new species models can be developed that will facilitate advances in the study of personality.

6. Ethical Note

All procedures were approved by the Department of Marine Resources, Bahamas (Permit no: MAF/LIA/22). After the experiment, sharks were released at their site of capture with their color tag removed. Sharks were kept for a maximum of 40 days to limit any potential impact of captivity. All manipulations (e.g. size/sex determination and tagging) were performed within 5 min to minimize handling stress. No steps required anaesthetizing the animals as this would increase manipulation time, increasing the stress on the animal.

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Declaration of Authorship

I, hereby, declare that this PhD thesis has been written only by the undersigned and that no sources other than those indicated have been used. This thesis has not been submitted for a doctor's degree at any other institution. I am aware of the underlying doctorate regulations of the faculty this thesis is submitted to, i.e., Faculty of Life Sciences of the Humboldt-University at Berlin.

Selbstandigkeitserklarung

Hiermit erkläre ich, die Dissertation selbständig und ohne unerlaubte Hilfe angefertigt zu haben. Ich habe mich nicht anderwärts als Doktorand beworben. Ich erkläre die Kenntnisnahme der dem Verfahren zugrunde liegenden Promotionsordnung der Landwirtschaftlich-Gärtnerischen Fakultät der Humboldt-Universität zu Berlin.

Minneapolis, den 15.02.2018

Jean Sebastien Finger